De la communauté à la méta-communauté, décrypter les patrons de diversité

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Contributions scientifiques

Diversité fonctionnelle des communautés végétales alpines et effets d'échelles

— **Chalmandrier, L.**, Münkemüller, T., Gallien, L., de Bello, F., Mazel, F., Lavergne, S. & Thuiller, W. 2013. A family of null models to distinguish between environmental filtering and biotic interactions in functional diversity patterns. Journal of Vegetation Science. 24, 853-864.

— **Chalmandrier, L.**, Münkemüller, T. , Colace, M.-P., Renaud J., Carlson, B. Z. , Choler, P., Clément, J.-C., Legay, N., Pellet, G., Saillard, A., Lavergne, S. & Thuiller, W. Spatial scale and intraspecific variability mediate the response of grassland trait diversity to alpine gradients. *en préparation*

— Siefert A., Violle, C., **Chalmandrier, L.**, Albert, C.H., Taudiere, A. et al. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *soumis* - Résumé en annexe.

Décomposition α, β, γ des nombres de Hill - extensions méthodologiques

— **Chalmandrier, L.**, Münkemüller, T., Lavergne, S. & Thuiller, W. Effects of species' similarity and dominance on the functional and phylogenetic structure of a plant meta-community. Ecology. 96 : 143-153

— **Chalmandrier, L.**, Münkemüller, T., Devictor, V., Lavergne, S. & Thuiller, W. Decomposing changes in phylogenetic and functional biodiversity across space and time. Methods in Ecology and Evolution. 6 : 109-118

— Thuiller, W., Guéguen, M., Georges, D., Bonet, R., **Chalmandrier, L.**, Garraud, L., Renaud, J., Roquet, C., Van Es, J., Zimmermann, N.E. & Lavergne, S. 2014. Are different facets of plant diversity well protected in the face of climate and land use changes ? A test study in the French Alps. Ecography. 37, 1254-1266 - Article en annexe.

Aspects méthodologiques de l'analyse des données de métabarcoding

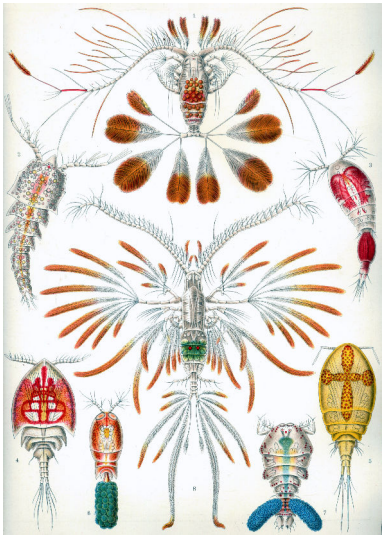
— **Chalmandrier L.**, Münkemüller, T., Lavergne, S., Thuiller, W. et al. Unravelling the invisible and quantifying the numerous : the promise of metabarcoding data for studying soil biotia diversity. *en préparation*

Introduction

« *What more delightful avocation than to take a piece of land and, by cautious experimentation, to prove how it works ?* »

Aldo Leopold

1 Contexte général



Copépodes planctoniques - [HAECKEL, 1904]

La diversité biologique, c'est-à-dire la variété du vivant, est l'une des caractéristiques les plus importantes des écosystèmes. Elle est depuis longtemps l'objet de nombreuses explorations, études scientifiques ou œuvres artistiques. Ainsi l'un des premiers balbutiements de la biologie moderne fut l'effort de classification entrepris par Linné pour révéler la structure existant dans le foisonnement d'êtres vivants aux formes variées. De fait, l'écologie, en tant que science, est caractérisée par la nécessité de décrire, inventorier, étudier et interpréter la diversité biologique à tous ses autres niveaux d'organisation. Depuis quelques années, l'ampleur sans précédent de l'érosion de la "biodiversité" en raison des activités humaines (changement climatique, d'usage de terres, invasions biologiques, PIMM et collab. [1995] ; ex. INGER et collab. [2014]) a mis la diversité des espèces et des écosystèmes au centre de l'attention des scientifiques et du public en général. Cela est dû à l'importance de la biodiversité dans le fonctionnement des écosystèmes et donc pour les sociétés humaines [COSTANZA et collab., 1998] et la nécessité de protéger cette diversité a été mise en avant pour justifier les initiatives de conservation [MYERS et collab., 2000]. Toutefois, il reste important de souligner que la diversité biologique ne constitue pas seulement un aspect pittoresque de la nature, mais un sujet scientifique central pour les écologues parce qu'elle témoigne de l'histoire, de la dynamique et des mécanismes de

fonctionnement des écosystèmes.

La notion de diversité est indissociable de la notion de “communauté” qui est la plus petite échelle à laquelle la diversité au sens classique (c'est-à-dire au niveau de l'espèce) puisse être étudiée. Telle que définie originellement par Möbius en 1877, une communauté est l'ensemble des organismes qui vivent et interagissent entre eux. Ses études sur les bancs d'huîtres montrèrent les liens forts existant entre êtres vivants ainsi que les propriétés de la communauté en tant que système biologique. Affirmant ainsi la nature holistique des communautés (comme proposé par CLEMENTS [1916]), il en fit des unités biologiques focalisant un intérêt et une approche scientifique. Comme décrite précédemment, leur diversité, c'est-à-dire leur richesse et leur variété [MAGURRAN, 2004; PIELOU, 1975] en est leur caractéristique la plus fondamentale.

À l'origine, la biodiversité est le produit de la diversification des êtres vivants. Les populations d'une espèce peuvent diverger au fur et à mesure qu'elles accumulent des mutations et des différences phénotypiques qui peuvent être neutres, mais peuvent aussi les rendre plus adaptées à différents environnements [AGUILÉE et collab., 2013; YAWATA et collab., 2014]. Parce que la diversité est partiellement le produit de l'adaptation aux différences d'environnement abiotique et biotique où vivent les espèces, l'étude des patrons de diversité peut nous informer sur les processus écologiques qui ont lieu ou qui ont eu lieu dans les communautés [RICOTTA, 2005; SUGIHARA, 1982].

Quand on parle de “patron de diversité”, on se réfère en fait plus précisément à la structure des communautés, c'est à dire à la valeur et la distribution de leur diversité ainsi que la différenciation en terme de composition des communautés dans l'espace et dans le temps. Une grande variété de processus déterministes et stochastiques sont susceptibles d'être à l'origine de ces patrons de diversité [GRAVEL et collab., 2006] et le principe derrière l'étude de ces patrons de diversité est que leur analyse permet leur inférence. D'après le cadre d'analyse de VELLEND et collab. [2014], on peut distinguer quatre types de processus fondamentaux. (1) Les processus de sélection des espèces par l'environnement. De nature déterministe, leur existence est due au fait que les espèces n'ont pas la même capacité à persister dans un environnement abiotique ou biotique donné. De fait cette notion est intrinsèquement liée à celle de niche écologique que l'on détaillera plus bas. (2) Les processus de spéciation par lesquels de nouvelles espèces apparaissent dans une région. (3) La dérive écologique qui se réfère à la stochasticité de la démographie des espèces et peut structurer un patron de diversité par hasard et (4) la dispersion, c'est-à-dire le déplacement d'individus dans l'espace d'une communauté à l'autre.

Cette thèse se focalise principalement sur la dichotomie entre processus déterministes et stochasticité. Ils sont intrinsèquement liés à la notion de niche écologique des espèces et à la stochasticité liée à la notion de dérive écologique. On abordera ensuite la question de la dispersion ; nous ne traiterons pas du sujet de la spéciation qu'en général on associe davantage à des échelles spatiales et temporelles plus importantes que celles abordées dans cette thèse [CAVENDER-BARES et collab., 2009; MACARTHUR et WILSON,

1967].

Les communautés végétales alpines sont un cas d'étude intéressant pour étudier les patrons de diversité. En effet, les milieux montagnards sont caractérisés par d'importants gradients environnementaux, notamment la baisse de température avec l'altitude, qui contraignent fortement l'assemblage des communautés. L'une des descriptions pionnières des patrons écologiques est ainsi l'étagement de la végétation avec l'altitude, décrite dès le tournant du XIXe siècle par von Humboldt. Cette observation classique implique que les communautés végétales sont soumises à des gradients abiotiques abrupts et permanents qui affectent fortement leur diversité et leur changement de composition dans l'espace. Cela fournit aussi une perspective prometteuse intéressante dû au fait que ce sont souvent les milieux tropicaux qui ont servi à formuler une part importante du corpus théorique des patrons de diversités [CONNELL, 1978; DIAMOND, 1975; HUBBELL, 2001; WEBB et collab., 2002], c'est-à-dire des milieux plus riches en espèces où les gradients environnementaux contraignent moins l'assemblage des communautés [MYERS et collab., 2013].

Étant donné que les communautés végétales alpines ont été l'objet d'étude principal de mon travail de thèse, je me servirai de ce cas particulier pour illustrer le reste de cette introduction.

2 La niche écologique et son estimation via les traits et la phylogénie

2.1 La notion de niche écologique

Hutchinson définit la niche comme un hypervolume à n dimensions, chaque dimension représentant une variable environnementale indépendante tel que la température, les ressources... [HUTCHINSON, 1957]. L'hypervolume représente alors les conditions environnementales dans lesquelles une espèce est capable de persister indéfiniment. L'intérêt de caractériser simultanément la niche sur plusieurs dimensions est double, tout d'abord cela permet de mieux caractériser la niche en prenant en compte de multiples variables potentiellement indépendantes, par ailleurs, cela permet de mieux caractériser les différences de niches entre espèces : deux espèces peuvent sembler partager les mêmes préférences sur les dimensions prises individuellement, mais avoir des niches complètement différentes dans un espace multi-dimensionnel [CLARK et collab., 2011]. On distingue la "niche fondamentale" de "la niche réalisée", cette dernière étant représentée par l'hypervolume des conditions environnementales où une espèce est effectivement observée et qui peut être en partie différent de celui de la niche fondamentale. Plusieurs facteurs écologiques peuvent expliquer ces différences : interactions biotiques positives ou négatives, limitation de la dispersion, perturbations... [PULLIAM, 2000]. Ces facteurs restreignent (par exemple, si une espèce est exclue d'un type d'habitat par la présence

d'une espèce compétitrice) ou étendent la niche écologique de l'espèce (par exemple si grâce à la facilitation, une espèce peut persister dans un environnement qui ne lui est pas favorable). Le problème de la confusion entre niche fondamentale et niche réalisée est que cela peut amener à confondre différents processus écologiques. Ainsi si une espèce est absente d'un site, il n'est pas possible de savoir avec cette unique information si cette absence est due au stress abiotique, à son exclusion par des espèces plus compétitives ou au hasard. Il est donc nécessaire d'avoir une information complémentaire pour estimer la niche fondamentale de l'espèce.

Cette estimation n'a rien d'évident, il a ainsi été proposé d'adopter une approche mécaniste de la niche écologique. Par exemple, on peut étudier l'écophysiologie d'une espèce pour estimer sa niche fondamentale et prédire sa distribution spatiale théorique le long des gradients climatiques (ex. KEARNEY et PORTER [2004]. C'est cette idée que l'information sur la niche écologique est contenue dans les caractéristiques des espèces au sens large (physiologie, morphologie, lignée évolutive...) qui est utilisée dans l'analyse des patrons de diversité fonctionnelle et phylogénétique. Le défi est alors d'obtenir des mesures qui soient effectivement liées à la niche écologique et qui soient suffisamment étudiées ou faciles à étudier pour permettre de décrire la majorité des espèces du système étudié. À titre d'exemple, l'étude citée auparavant [KEARNEY et PORTER, 2004] nécessita une expérimentation en laboratoire de la tolérance climatique d'une espèce de lézard. Bien que déjà important, un tel protocole ne permet de mesurer "que" quelques paramètres liés aux conditions environnementales et pas l'ensemble des conditions écologiques dans lesquelles cette espèce vit (interactions compétitives, résistance aux perturbations...) et est de plus limité à une unique espèce.

C'est pourquoi deux méthodes principales ont été proposées pour décrire plus facilement la similarité de niche des espèces : l'approche fonctionnelle, qui estime la différence de niches à partir des caractères biologiques des espèces, c'est-à-dire leurs traits fonctionnels [LAVOREL et GARNIER, 2002; VIOLLE et collab., 2007] et l'approche phylogénétique qui se base sur les distances évolutives entre espèces [WEBB et collab., 2002].

2.2 Les traits fonctionnels - lien avec la stratégie écologique

On peut définir un trait fonctionnel comme étant un trait morphologique, physiologique ou phénologique ayant un impact indirect sur la valeur sélective de l'individu, que l'on peut évaluer par l'observation de la croissance, la reproduction et la survie des individus [LAVOREL et collab., 1997; VIOLLE et collab., 2007]. On distingue fréquemment ensuite les traits dits "de réponse", qui répondent aux changements des conditions de l'environnement et les traits dits "d'effet" qui modifient l'environnement de l'individu. Cette dichotomie met en valeur les objectifs principaux de l'écologie fonctionnelle et a été formalisée par LAVOREL et GARNIER [2002] pour unir la vision "réponse" des traits directement héritée de la théorie des filtres d'assemblage [KEDDY, 1992] et la vision "effet"

qui s'attache plus à lier la communauté au fonctionnement des écosystèmes [TILMAN et collab., 1997]. Au final, il s'agit essentiellement d'une conceptualisation de l'écologie fonctionnelle étant donné que la plupart des traits classiquement utilisés en écologie végétale sont à la fois des traits de réponse et des traits d'effet [LAVOREL et GARNIER, 2002].

Les traits fonctionnels fréquemment étudiés sont des traits dits "soft", c'est-à-dire facilement mesurables et donc plus susceptibles de constituer des jeux de données importants. Ils ont un rapport direct à la physiologie de l'individu [RODERICK et collab., 1999] mais souvent indirect à la fitness des individus, et donc la démographie des populations [SILVERTOWN et collab., 1992]. On leur oppose les traits fonctionnels dits "hard", tel le taux de croissance, eux directement liés à la fitness des individus. Néanmoins, les deux types de traits sont souvent corrélés ce qui justifie l'approche par traits "soft" [LAVOREL et GARNIER, 2002].

Dans le cadre spécifique de cette thèse, des traits fonctionnels "soft" sont utilisés pour caractériser la niche écologique des espèces (cf. Tableau 1), ce qui s'inscrit dans une vision plutôt "réponse". Dans le cas des plantes, le lien entre traits et écophysiologie a été démontré très tôt de manière empirique [REICH et collab., 1999], et plus récemment aux notions de valeur sélective et de traits d'histoire de vie [ADLER et collab., 2014]. De plus, le lien entre variations de traits fonctionnels et variations de l'environnement à de multiples échelles spatiales montre celui existant entre traits et niche écologiques [THUILLER et collab., 2004; WRIGHT et collab., 2004]. Enfin, l'étude de la variabilité des traits fonctionnels entre plantes partageant le même environnement a montré que les traits fonctionnels ne témoignent pas seulement de l'impact de l'environnement sur la physiologie des plantes mais aussi de stratégies écologiques différentes entre plantes pour répondre au même environnement (ex. HOBBIE et HÖGBERG [2012]). Par ailleurs, l'étude de l'évolution des traits fonctionnels a également montré comment ces derniers témoignent de l'émergence de nouvelles stratégies écologiques, notamment de nouvelles formes de vie [FLORES et collab., 2014; MOLES et collab., 2005; STOCK et VERBOOM, 2012] ou de l'adaptation des plantes à de nouveaux habitats [ZANNE et collab., 2014].

Parce que le concept de niche écologique implique une multi-dimensionnalité, il a été proposé d'utiliser plusieurs traits fonctionnels de concert pour ainsi capter les différentes dimensions de la niche et estimer un syndrome fonctionnel. Cette approche est d'autant plus appropriée que s'il existe des corrélations importantes entre traits reflétant des compromis, certains sont indépendants et sont donc susceptibles de refléter des axes différents de la niche écologique des espèces [DÍAZ et CABIDO, 1997]. Ainsi WESTOBY [1998] proposa de caractériser la niche écologique des plantes via le syndrome LHS ("Leaf-Height-Seed"), permettant une adaptation du triangle de GRIME [1977] à l'étude des traits fonctionnels. Ce dernier caractérise trois stratégies écologiques majeures chez les plantes : compétitrice, rudérale, stress. WESTOBY [1998] montra comment l'utilisation conjointe de traits fonctionnels liés à la hauteur, à l'économie foliaire et aux caractéristiques reproductrices permet de retrouver le cadre d'analyse de Grime. Le syndrome

TABLEAU 1 – Traits fonctionnels étudiés durant la thèse

Trait fonctionnel	Quantification	Stratégie écologique si la valeur du trait est élevée	Références
Hauteur végétative	Hauteur de la canopée	Compétitrice pour la lumière	VIOLLE et collab. [2009]
SLA	Surface foliaire/masse sèche foliaire	Tissus foliaires peu denses. Taux de photosynthèse élevé. Acquisition rapide de nutriments. Croissance rapide. Intolérance au stress.	REICH et collab. [1999] VIOLLE et collab. [2009] GROSS et collab. [2009]
LDMC	masse sèche foliaire /masse fraîche foliaire	Tissus foliaires denses et longévifs. Croissance lente. Tolérance au stress.	POORTER et BERGKOTTE [1992] WEIHER et collab. [1999]
LCC	Contenance foliaire en carbone	Croissance lente	POORTER et BERGKOTTE [1992]
LNC	Contenance foliaire en azote	Acquisition rapide en azote	REICH et collab. [1999] PÉREZ-RAMOS et collab. [2012]
δ^{13}C foliaire	Contenance en ^{13}C/contenance en isotope ^{12}C - valeur standard (CO_2 atmosphérique)	Efficacité de l'utilisation de l'eau. Efficacité photosynthétique face à la baisse de pression partielle en CO2.	SILIM et collab. [2001] LIU et collab. [2014]
δ^{15}N foliaire	Contenance en ^{15}N/contenance en isotope ^{14}N - valeur standard (N_2 atmosphérique)	Racines profondes. Type de mycorhization (Aucune > endomycorhizes > ectomycorhizes > ectendomycorhizes) Acquisition en ammonium vs. nitrate (dans les toundras alpines).	MILLER et BOWMAN [2002] HOBBIE et HÖGBERG [2012]
Masse des graines		Faible nombre de graines. Faible distance de dispersion. Longévité des propagules Taux de survie élevés des plantules.	WESTOBY [1998] WEIHER et collab. [1999] EHRLÉN et ERIKSSON [2000]

"LHS" fut par la suite mis en pratique dans de nombreuses études [DE BELLO et collab., 2013; LAVERGNE et collab., 2003].

2.3 La phylogénie comme proxy de la niche

Le lien entre distances phylogénétiques et similarité de niche est (encore) plus indirect que le lien entre traits fonctionnels "soft" et similarité de niche. L'environnement n'agit pas sur l'identité phylogénétique des individus, mais sur leur phénotype qui résulte lui de processus évolutifs [LAVERGNE et collab., 2010]. Elle s'appuie sur de nombreuses constatations que des espèces proches sont plus similaires écologiquement que des espèces éloignées, ce qui a été noté depuis DARWIN [1859]. C'est en se basant sur ces travaux qu'il a été affirmé que la phylogénie peut être un meilleur proxy de la similarité écologique entre espèces si les traits à l'origine cette similarité écologique ne sont pas connus ou pas mesurés [MOUQUET et collab., 2012; WEBB et collab., 2002]. Cependant, l'hypothèse que l'on peut estimer la niche des espèces grâce à la phylogénie est controversée. Pour que cette hypothèse soit vérifiée, il faut que la niche écologique présente un signal phylogénétique, c'est-à-dire que des espèces proches soient effectivement plus similaires que des espèces prises au hasard dans la phylogénie [BLOMBERG et collab., 2003; LOSOS, 2008]. Pour qu'un tel signal apparaisse, il n'est pas nécessaire de supposer l'existence de processus évolutifs particuliers comme la sélection stabilisante ou des taux d'évolution faible [MOUQUET et collab., 2012]. En effet, si on suppose un simple modèle d'évolution par mouvement brownien de multiples traits liées à la niche (c'est-à-dire que le long de la phylogénie, entre deux pas de temps, la différence de valeurs du trait suit une loi normale centrée d'écart-type constant), ce modèle génère une relation linéaire entre distance phylogénétique et la racine de la distance dissimilarité de niche (Figure 1, LETTEN et CORNWELL [2014]; MÜNKEMÜLLER et collab. [2015].

Par ailleurs, plus empiriquement, il a été montré à maintes reprises que les patrons de diversité phylogénétique ne sont pas aléatoires, ce qui exclut l'hypothèse que la niche écologique est complètement indépendante de la phylogénie (ex. CAVENDER-BARES et collab. [2004]). De plus, certains traits fonctionnels connus pour être importants dans l'étude de l'assemblage des communautés présentent un signal phylogénétique [FLORES et collab., 2014]. Enfin dans certains cas, les patrons de diversité phylogénétique ont pu être liés à des caractéristiques phénotypiques [VIOLLE et collab., 2011] donnant alors une perspective complète sur l'impact présent de l'héritage évolutif des espèces et des contraintes qu'il peut poser sur l'assemblage des communautés.

Au final, les patrons de diversité fonctionnelle et phylogénétique se sont pas nécessairement similaires, mais de nombreuses études ont montré que l'analyse des deux types de patrons en parallèle apporte des réponses complémentaires sur l'impact de l'héritage évolutif des espèces et de certains traits phénotypiques sur l'assemblage des communautés [DEVICTOR et collab., 2010; SAFI et collab., 2011].

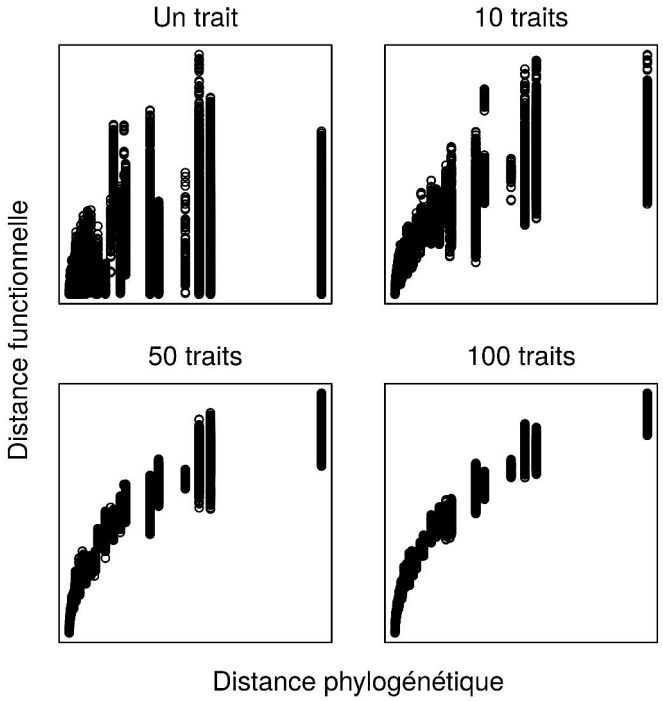


FIGURE 1 – Lien entre distances phylogénétiques et fonctionnelles calculées à partir de un, dix, cinquante et cent traits. La phylogénie ultramétrique comportait 200 espèces et les traits évoluaient le long des branches en suivant un mouvement brownien.

3 Règles d'assemblage

Une fois la niche estimée, il devient possible de faire des hypothèses sur la façon dont différents processus écologiques sont susceptibles de l'influencer et quelle en sera la conséquence sur la structure de la diversité des communautés observées. Le principe général de l'étude des règles d'assemblage est l'idée que les communautés sont des sous-échantillons d'espèces présentes dans un pool régional d'espèces [CORNELL et HARRISON, 2014]. En général, on définit ce pool comme "régional" et comprenant les espèces présentes dans la région à cause de contingences biogéographiques ou historiques. Les espèces du pool régional sont alors considérées susceptibles de disperser dans les communautés étudiées [RICKLEFS, 2004]. Les communautés observées sont ensuite le résultat d'une succession de filtres liés à différents processus écologiques (ex. : compétition, facilitation, dispersion, environnement) appelés "règles d'assemblage" qui font que les communautés ne sont pas forcément des échantillons aléatoires des espèces du pool régional [DIAMOND, 1975; KEDDY, 1992]. On peut alors caractériser le patron de diversité, la structure, des communautés.

Si certaines communautés observées présentent une structure non aléatoire, on peut interpréter qu'une règle d'assemblage particulière agit sur elles. Ainsi si les communautés observées sont moins diverses que ce qu'on attend d'échantillons aléatoires du pool régional, on parle de communautés convergentes ; si elles sont plus diverses que ce qu'on

attend d'échantillons aléatoires du pool régional, on parle de communautés divergentes.

De la même façon que l'on peut interpréter la structure de la diversité contenue au sein de chaque communauté, il est également possible d'interpréter d'autres facettes relatives à l'ensemble de la méta-communauté. Pour cela, WHITTAKER [1960] suggéra de décomposer la diversité d'une méta-communauté en plusieurs composantes spatiales : la diversité moyenne contenue dans les communautés (diversité α), la diversité régionale (diversité γ) et la diversité en communautés (diversité β), aussi appelée "community turnover", "communitiy dissimilarity"... Populaire, cette méthodologie est utile pour étudier les processus écologiques à l'origine de la structure des méta-communautés [SPASOJEVIC et collab., 2014; SWENSON et collab., 2011].

Si le patron de diversité de certaines communautés ou de la méta-communauté dans son ensemble présentent une structure non aléatoire, cela est interprété comme le résultat d'une règle d'assemblage à un processus écologique particulier (Figure 2).

3.1 Filtre abiotique

Il contraint la composition d'une communauté aux espèces pouvant y persister malgré les conditions abiotiques locales, c'est-à-dire aux espèces dont la niche écologique comprend les conditions abiotiques locales. Cette définition réfère alors stricto sensu à la niche fondamentale des espèces, c'est-à-dire aux conditions de stress abiotique que la physiologie de l'espèce peut supporter. En termes de patrons de diversité, il y a un consensus dans la littérature pour affirmer qu'une communauté soumise à un stress abiotique important aura une plus faible diversité et une diversité convergente, que ce soit phylogénétiquement ou fonctionnellement [CORNWELL et ACKERLY, 2009; WEBB et collab., 2002; WEIHER et KEDDY, 1995]. Cela s'explique par le fait que la survie en milieu stressant nécessite qu'une espèce ait un phénotype adapté (ex. résistance au froid). Ainsi seulement un nombre limité d'espèces du pool régional est capable de s'y implanter et ces espèces ont tendance à être similaires écologiquement, ce qui est susceptible de se traduire en une diversité taxonomique, fonctionnelle et phylogénétique réduite. Pour la même raison, une méta-communauté comportant des gradients environnementaux importants aura tendance à avoir une diversité β importante car les communautés seront fortement différenciées en raison des différences de conditions environnementales (Figure 2, b).

Les milieux alpins sont caractérisés par d'importants gradients environnementaux principalement liés à l'altitude, l'exposition et la topographie. Il est connu que les traits fonctionnels des plantes sont affectés par ces gradients environnementaux de multiples manières [KÖRNER, 2003]. Par exemple, avec la baisse de température, on observe que les plantes des communautés végétales investissent différemment le carbone acquis via la photosynthèse avec une partie aérienne moins volumineuse que la partie souterraine, expliquant la diminution de la taille des espèces à taux de photosynthèse équivalent. Cela s'explique par plusieurs facteurs : le froid ralentit le métabolisme des parties aériennes, li-

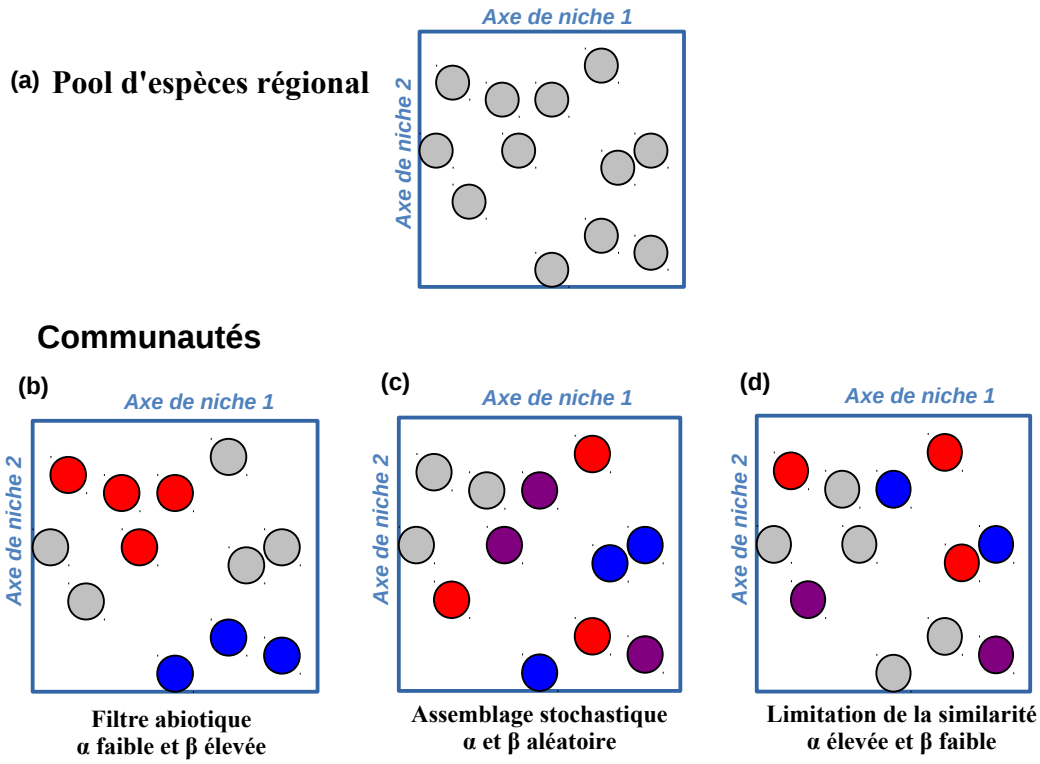


FIGURE 2 – Conséquences des règles d'assemblage sur le patron de diversité des communautés. Les cercles représentent les espèces du pool de référence placées dans un espace à deux dimensions (carré bleu) caractérisant leur similarité écologique. On considère deux communautés rouge et bleue situées dans des conditions abiotiques différentes. Elles s'assemblent à partir du pool régional (a) et sont constituées des espèces rouges et bleues et ont en commun les espèces violettes. On distingue trois cas (b), (c) et (d). Dans le cas (b), le filtre abiotique est prédominant : les communautés sont alors composées d'espèces similaires (faible diversité α) et ont des compositions différentes (diversité β élevée) Dans le cas (c), l'assemblage est aléatoire et il n'y a pas de patron de diversité particulier. Enfin, dans le cas (d) la limitation de la similarité est prédominante, les communautés sont alors composées d'espèces dissimilaires (diversité α élevée) et sont similaires entre elles car possédant une combinaison proche d'espèces compétitives (diversity β faible). Ces communautés aléatoires permettent d'estimer la distribution de l'indice de diversité sous l'hypothèse nulle. La diversité observée (d) lui est ensuite comparée. Selon sa place dans la distribution nulle, on peut conclure que la communauté est convergente, aléatoire ou divergente.

mitant ainsi leur croissance et le caractère adaptatif de la stature prostrée qui permet une plus grande proximité au sol, plus chaud que l'air ambiant [MEYER et collab., 2008]. Un autre exemple est la plus grande efficacité photosynthétique des plantes alpines par rapport aux plantes non alpines en réponse à la baisse de la pression partielle en CO2, [KÖRNER, 2003]. Une conséquence de cette efficacité photosynthétique accrue est une baisse de la discrimination par la Rubisco de l'isotope de carbone 13 (plus lourd que le carbone 12), ce qui effectivement abouti à une augmentation du ratio δ^{13}C dans les feuilles des plantes alpines (Table 1).

En plus des gradients à large échelle spatiale, la méso-topographie des paysages alpins (pente, position topographique...) est susceptible de générer des gradients locaux. On peut décrire ce gradient comme allant de zones de crêtes exposées au vent et moins enneigées à des zones d'accumulation de neige. Ce gradient implique des différences de conditions abiotiques au niveau de la durée de saison de croissance : dessiccation par le vent, humidité du sol et disponibilité en azote [KÖRNER, 2003] ;CARLSON et collab. [2015]; CHOLER [2005]. Il a un impact non négligeable sur les patrons de diversité fonctionnelle des communautés végétales alpines [CHOLER, 2005] et peut donc se superposer au patron de diversité généré par les gradients environnementaux à large échelle spatiale [DE BELLO et collab., 2013].

3.2 Interactions biotiques

Lorsque deux espèces sont localement en compétition pour la même ressource, on prédit que l'une va prendre le pas sur l'autre et la faire disparaître : on parle alors d'exclusion compétitive. C'est un résultat ancien des premières études théoriques de systèmes écologiques réalisées par Lotka et Volterra et plus tard testé expérimentalement par Gause (1936). Néanmoins si on pousse la logique de ce principe jusqu'au bout, il entre en contradiction avec le fait que les communautés, qu'on réduira ici à un unique niveau trophique, sont typiquement composées d'un grand nombre d'espèces en coexistence malgré le fait qu'elles exploitent les mêmes ressources.

Deux mécanismes ont été proposés pour expliquer cette stabilité de la coexistence [ADLER et collab., 2007; CHESSON, 2000]. Le premier est que les espèces en coexistence ont des niches trop dissimilaires pour que la compétition interspécifique soit suffisamment intense. En d'autres termes, la compétition est alors plus intense entre individus de la même espèce (qui partagent des niches proches) plutôt qu'entre individus d'espèces dissimilaires (Figure 2, d). Grâce à ce mécanisme, on prédit que si la compétition est le principal mécanisme contraignant sa diversité, une communauté sera composée d'espèces dissimilaires et donc qu'elle sera fonctionnellement ou phylogénétiquement divergente. Ce principe de *limitation de la similarité* est le principal paradigme utilisé en analyse de patrons de diversité pour décrire l'impact de la compétition.

Le deuxième mécanisme est *l'équivalence de valeur sélective* entre espèces (ou compé-

tition hiérarchique) : si deux espèces partagent la même niche, elles ne peuvent coexister que si leurs valeurs sélectives sont exactement égales. C'est un cas qui paraît irréaliste, mais si des espèces ont une valeur sélective proches, il suffit alors d'une petite différence de niche pour que leur coexistence soit stable [CHESSON, 2000]. À l'inverse du précédent, ce mécanisme prédit que les communautés où la compétition est intense devraient être composées d'espèces écologiquement similaires [MAYFIELD et LEVINE, 2010] et donc être fonctionnellement ou phylogénétiquement convergentes.

Théoriquement la coexistence des espèces est déterminée par l'action conjointe de ces deux mécanismes. Mais en pratique seule la limitation de la similarité est utilisée pour interpréter les patrons de diversité. L'interprétation de la diversité α au sein des communauté peut alors se réduire à la dichotomie entre (1) un filtre abiotique favorisant la convergence au sein des espèces au sein des communautés et (2) à l'inverse un filtre compétitif favorisant plutôt leur divergence. Dans ce cadre d'analyse, le fait que le filtre compétitif puisse, comme le filtre abiotique, favoriser la coexistence d'espèces similaires est problématique, expliquant pourquoi que ce mécanisme a souvent été ignoré [MAYFIELD et LEVINE, 2010].

Les interactions biotiques peuvent être aussi positives et se manifester par de la facilitation. Cela se traduit par la coexistence locale d'individus dont au moins un des deux bénéficie de l'interaction et aucun en n'est désavantagé. En termes de patrons de diversité, on prédit que cela se manifeste par la co-occurrence à échelle spatiale très fine d'individus dissimilaires, avec l'individu facilitant possédant un trait permettant sa propre survie que le facilité ne possède pas [GROSS et collab., 2013].

Au sein des communautés végétales, la nature des interactions biotiques peut changer le long des gradients environnementaux, venant conforter la vision conceptuelle des interactions biotiques comme étant subordonnées au filtre abiotique [LAVERGNE et collab., 2010]. Un exemple classique de l'écologie alpine est l'hypothèse du gradient de stress [CALLAWAY et collab., 2002]. Lorsque deux plantes sont spatialement proches, elles interagissent négativement en étant en compétition pour les mêmes ressources (nutriments, lumière, eau, espace) mais aussi positivement car leur proximité permet une meilleure protection au vent ou aux températures trop faibles. Le bilan de ces deux interactions (compétition et facilitation) dépend de la situation de ces deux plantes sur le gradient de stress. CHOLER et collab. [2001] ont montré que dans des zones peu exposées au vent, la compétition est prépondérante car la protection au vent ne constitue pas un atout important au développement des individus. En revanche dans les zones exposées où le stress abiotique devient le mécanisme principal limitant la survie des individus, bénéficier de la protection d'un couvert végétal devient indispensable.

En résumé, on peut voir que les interactions biotiques sont nombreuses, subordonnées aux gradients environnementaux et peuvent diminuer (compétition hiérarchique) ou augmenter (limitation de la similarité, facilitation) la diversité des communautés.

3.3 La dispersion

Par rapport aux processus de niche décrits plus haut, l'influence de la capacité de dispersion des espèces a été qualifiée de processus semi-déterministe et semi-stochastique [VELLEND et collab., 2014]. L'étude de ces mécanismes s'inscrit dans le cadre d'étude de l'écologie des "méta-communautés", c'est-à-dire d'un ensemble de communautés reliées par des relations de dispersion entre leurs espèces [LEIBOLD et collab., 2004].

La dispersion correspond au déplacement d'une partie des individus hors de leur communauté pour s'implanter ailleurs. Dans le cas des plantes, c'est un processus qui s'effectue en général au niveau de la dispersion des graines. L'aptitude à la dispersion varie beaucoup d'une espèce à l'autre [THOMSON et collab., 2011], ce qui explique que la dispersion a une place intermédiaire dans le continuum des processus déterministes vs. stochastiques [VELLEND et collab., 2014]. En fait, la dispersion implique un degré de stochasticité, en particulier pour les plantes qui dispersent passivement, mais elle peut être aussi un élément important de la stratégie écologique d'une espèce, comme c'est le cas des plantes rudérales (*sensu* GRIME [1977]) qui sont caractérisée par une capacité de dispersion importante. Bien que sensibles à la compétition et au stress abiotique, elles peuvent persister dans un paysage en maintenant des populations dans des environnements perturbés (donc transitoires) ; l'aléa d'un tel mode de persistance est contrebalancé par la production d'un grand nombre de graines dispersant facilement permettant ainsi d'augmenter les chances que des propagagules atteignent des environnements favorables.

Si sa capacité de dispersion est limitée, une espèce n'occupe pas forcément l'ensemble des communautés que pourrait théoriquement le lui permettre sa niche écologique. C'est un phénomène qui affecte la distribution locale des espèces avec des zones d'habitat laissées inoccupées par des espèces dispersant peu [EHRLÉN et ERIKSSON, 2000]. Les espèces peuvent également occuper une distribution géographique restreinte. Par exemple, si son aire de distribution potentielle (c'est-à-dire celle dont les conditions environnementales lui sont favorables) s'est étendue trop récemment pour qu'elle ait eu le temps de la coloniser [SVENNING et SKOV, 2007], si des barrières géographiques ont empêché son expansion ou si tout simplement l'espèce est apparue récemment. Ce processus est susceptible de différencier la composition de communautés indépendamment des conditions abiotiques et biotiques similaires (Weinstein et al. 2014).

À l'inverse, une espèce avec une capacité de colonisation forte est susceptible de maintenir des populations dans des "communautés-puits" où les conditions abiotiques ou biotiques ne lui sont pas favorables par simple afflux de propagules depuis des "communautés-sources" où sa niche lui permet de persister [ANGERT, 2009]. Ce mécanisme peut alors contrebalancer des processus de niche différenciés entre communautés (par exemple des conditions abiotiques différentes) et "biaiser" le patron de diversité en homogénéisant leur composition [SIMONIS et ELLIS, 2014].

Pour résumer, on prédit que la dispersion introduit une structuration spatiale des patrons de diversité taxonomique indépendamment de la structuration de l'environnement. Son influence sur les patrons de diversité fonctionnelle et phylogénétique est en revanche moins claire. En première approximation, les prédictions relatives au patron de diversité fonctionnelle et phylogénétique peuvent refléter celles liées au patron de diversité taxonomique [SPASOJEVIC et collab., 2014], par exemple si les barrières à la dispersion contribuent à empêcher des lignées phylogénétiques et des groupes fonctionnels d'atteindre des environnements qui leur seraient favorables [WEINSTEIN et collab., 2014]. En revanche si la capacité de dispersion n'est pas liée aux traits fonctionnels étudiés ou à la phylogénie (par exemple s'il y a suffisamment de redondance fonctionnelle parmi les espèces étudiées pour que malgré la limitation de la dispersion, tout les traits fonctionnels puissent arriver dans les communautés), on peut alors s'attendre à des patrons de diversité fonctionnelle ou phylogénétique différents de celui de la diversité taxonomique [MÜNKEMÜLLER et collab., 2012; WEINSTEIN et collab., 2014].

3.4 Hasard et neutralité

Les différents mécanismes présentés précédemment dépeignent une vision déterministe de l'assemblage des communautés qui seraient générées par la variabilité des niches et des capacités de dispersion différentes entre espèces. À contre-pied, HUBBELL [2001] émit l'hypothèse que les espèces d'un niveau trophique donné puissent être considérées équivalentes en termes de démographie (mêmes taux de natalité, mortalité et taux de dispersion) quelles que soient les conditions abiotiques ou biotiques locales, c'est-à-dire comme ayant les mêmes caractéristiques de niche. Dans ce cadre, les patrons de diversité émergent alors par hasard via des événements de spéciation, d'extinction et d'immigration. Conceptuellement, le modèle neutre de Hubbell introduit ainsi la stochasticité et la limitation de la dispersion comme une explication possible de patrons de diversité non aléatoire sans supposer qu'ils sont dus à des différences de niches écologiques entre espèces [JABOT et CHAVE, 2009; VOLKOV et collab., 2003].

Bien que derrière cette "stochasticité" puissent se cacher des mécanismes déterministes non caractérisés [CLARK, 2009], on peut considérer l'assemblage des communautés comme étant placé sur un continuum entre des processus déterministes décrits plus haut et une part de hasard due à la stochasticité démographique des individus peuplant les communautés [GRAVEL et collab., 2006; VELLEND et collab., 2014].

4 Mesurer et tester la diversité

4.1 Démarche générale

Basée sur cette vision de l'assemblage des communautés, l'approche statistique classique pour étudier un patron de diversité se résume à trois éléments principaux : l'indice

de diversité, le pool d'espèces et le modèle nul. Elle est basée sur l'idée de tester si les communautés observées sont des échantillons aléatoires de l'ensemble des espèces présentes dans la région (c.a.d. le pool régional).

Pour réaliser cette analyse, un indice est choisi pour quantifier une caractéristique de la communauté ou de la méta-communauté observée. Ensuite, un modèle nul génère un ensemble de communautés ou méta-communautés aléatoires qui se conforment à l'hypothèse nulle de l'étude. En général, ces modèles contiennent certaines contraintes (par exemple dans la Figure 3, toutes les communautés aléatoires possèdent le même nombre d'espèces). Chaque communauté ou méta-communauté aléatoire est caractérisée par un indice générant ainsi une distribution nulle de cet indice sous l'hypothèse nulle. À cette distribution est comparée l'indice effectivement observé. Selon la place de cet indice dans la distribution nulle ainsi générée, on peut alors savoir si le patron de diversité de la communauté ou la méta-communauté est significativement différent de ce qu'on attend sous l'hypothèse nulle. On infère alors la ou les règles d'assemblage qui en sont à l'origine. Dans le cas de la diversité fonctionnelle ou phylogénétique contenue dans une communauté, si cette dernière est plus basse qu'attendue sous l'hypothèse d'un échantillonnage aléatoire du pool d'espèce, on parlera d'une communauté fonctionnellement convergente. À l'inverse, si la diversité est plus élevée qu'attendue, on parle d'une communauté fonctionnellement divergente. Le même raisonnement s'applique à la diversité phylogénétique.

4.2 Choisir un indice

L'estimation de la diversité taxonomique, fonctionnelle et phylogénétique est sujette à de nombreux débats et cette question a généré un important corpus d'indices de diversité (cf. TUOMISTO [2010], PAVOINE et BONSALL [2011] pour un bilan) ; et ce, malgré le fait que ces indices sont souvent redondants (MOUCHET et collab. [2010] ; ex. LALIBERTÉ et LEGENDRE [2010]). MAGURRAN [2004] définit la diversité d'une unité (communauté, région...) comme étant une mesure prenant en compte à la fois (1) la richesse d'une communauté, c'est-à-dire le nombre d'espèces et (2) la régularité de la communauté, c'est-à-dire la répartition des abondances au sein de la communauté. À cela, on peut ajouter une troisième composante spécifique de l'étude des diversités fonctionnelle et phylogénétique : (3) la similarité entre espèces. Certains auteurs ont cherché à ne quantifier qu'une partie de ces caractéristiques (ex. VILLÉGER et collab. [2008]) et il a été proposé de classifier la plupart des mesures de diversité en fonction de la ou des caractéristiques de la diversité qu'elles quantifient [PAVOINE et BONSALL, 2011].

Dans le cadre de la thèse, je me suis limité à l'étude et l'utilisation des indices de diversité dits "nombres effectifs" ou nombres de HILL [1973], tels que les définit JOST [2006] : ce sont des mesures prenant en compte les trois caractères évoqués précédemment et dont la valeur est maximale quand les espèces d'une communauté sont complètement dissi-

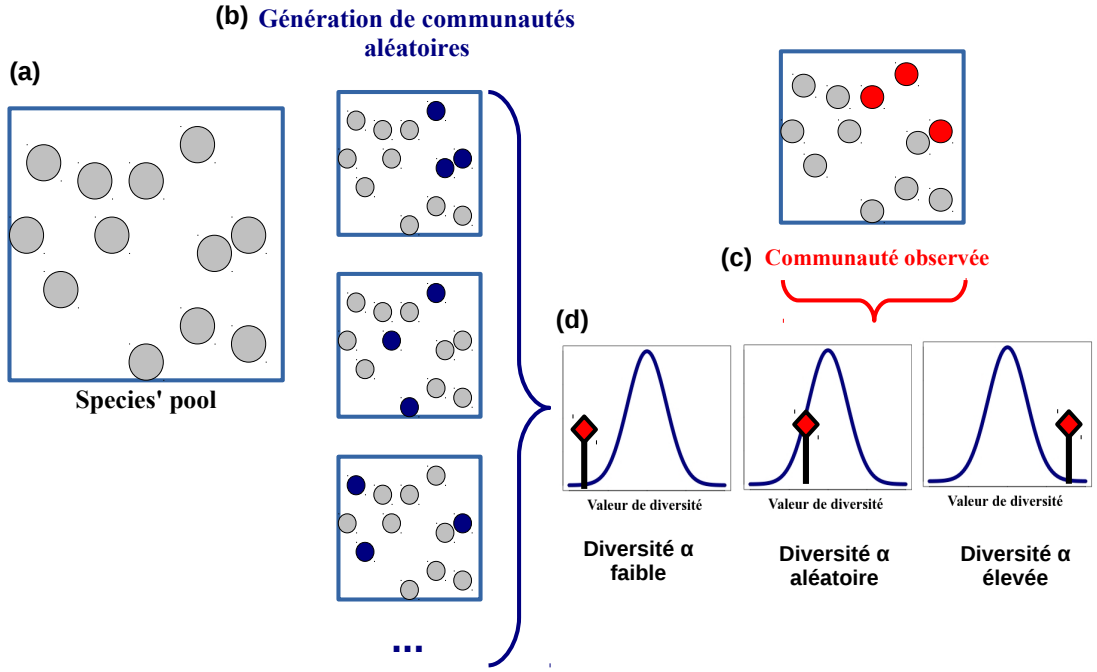


FIGURE 3 – Démarche analytique pour tester la diversité d'une communauté observée. Les cercles représentent les espèces du pool de référence placées dans un espace à deux dimensions (carré bleu) caractérisant leur similarité écologique. On cherche à tester la diversité de la communauté observée (c) dans laquelle les espèces rouges ont été observées. À partir d'un pool d'espèces (a), un modèle nul génère une série de communautés aléatoires (b) suivant une hypothèse nulle. Le cas dépeint est celui d'un modèle nul gardant constante le nombre d'espèces dans les communautés aléatoires. Ces communautés aléatoires permettent d'estimer la distribution de l'indice de diversité sous l'hypothèse nulle. La diversité observée (d) lui est ensuite comparée. Selon sa place dans la distribution nulle, on peut conclure que la communauté est convergente, aléatoire ou divergente.

milaires et en égales proportions. Alors la diversité est numériquement égale au nombre d'espèces. Ces indices ont été l'objet de tentatives d'unification pour proposer des familles d'indices de diversité [CHAO et collab., 2010; LEINSTER et COBBOLD, 2012; PAVOINE et collab., 2009] que nous verrons plus en détail dans la partie 2.

4.3 Choisir un pool d'espèce

Théoriquement, il représente le pool régional d'espèces avec la définition biogéographique qui a été défini auparavant : l'ensemble des espèces présentes dans la région à cause de contingences biogéographiques ou historiques et pouvant disperser dans les communautés étudiées. Dans les faits, par défaut, il représente souvent l'ensemble des espèces échantillonnées pour constituer le jeu de données étudié. Il peut y avoir d'autres définitions liées à des objectifs d'analyse particuliers : par exemple être réduit aux espèces d'un habitat d'une région [DE BELLO et collab., 2012; ZOBEL et collab., 2011]. C'est pourquoi la définition la plus conservatrice du pool d'espèce est probablement "l'ensemble des espèces randomisées par le modèle nul".

4.4 Choisir un modèle nul

Ces modèles nuls peuvent prendre de nombreuses formes ; dans son étude, HARDY [2008] compara différents modèles nuls et leur erreur de Type I dans la détection de patrons de diversité phylogénétique de communautés neutres. Comme mentionné précédemment, il montra que ces modèles nuls, de par la nature de l'algorithme les générant, ne sont pas complètement aléatoires et conservent un certain nombre de contraintes et par conséquent ont des hypothèses implicites. Cela entraîne des différences des modèles nuls en termes d'erreur de Type I (en l'occurrence de ne pas diagnostiquer un patron de diversité phylogénétique significativement différent de l'aléatoire quand l'assemblage est neutre). Par exemple, un des modèles les plus classiques proposés par WEBB et collab. [2002] pour tester les patrons de diversité phylogénétique consiste à mélanger les colonnes de la matrice sites/espèce. Hardy montra que ce modèle nul est l'un des plus robustes en terme d'erreur de type I sous certaines conditions. Ce modèle nul garde donc constante la structure de la matrice site/espèces (richesse spécifique et patrons d'abondance par site, fréquence d'une espèce dans la méta-communauté...) et ne mélange que l'identité des espèces sur la phylogénie. Ainsi ces dernières constituent la caractéristique effectivement rendue aléatoire par le modèle et qui est donc testée par le modèle nul.

5 Présupposés lors de l'analyse de patrons de diversité

Ces présupposés sont principalement dus à la définition parfois vague et arbitraire de la "communauté" [RICKLEFS, 2008]. FAUTH et collab. [1996] ont ainsi souligné que si la définition théorique d'une "communauté" soit claire, les écologues définissent en fait

de communauté, ce que FAUTH et collab. [1996] qualifient “d’ensemble”, c’est-à-dire un groupe d’espèces (1) coexistant spatialement, (2) appartenant à une même guilde (par exemple, “les arbres”, ou “les pollinisateurs”) et (3) appartenant à une même lignée phylogénétique (par exemple, “les mammifères” ou “les angiospermes”).

À ceci, on peut rajouter la méthodologie d’étude (4) du patron de diversité, c’est-à-dire le triptyque simple “pool d’espèces - indice de diversité - modèle nul” qui est susceptible d’infinies variations et d’autant de suppositions.

La remise en cause de ces différents présupposés (à part le point (2)) est le fil rouge du travail effectué durant cette thèse et sera abordé au travers de ses trois chapitres.

Partie 1 : Diversité fonctionnelle des communautés végétales alpines et effets d’échelles

Le point (1) rejoint la problématique d’échelle spatiale, c’est à dire à la surface spatiale sur laquelle sont définies la communauté et la surface géographique de la “région” qui sert à définir le pool d’espèces. Et le point (3) à la problématique d’échelle organisationnelle, c’est-à-dire le niveau taxonomique auquel est identifié un individu (individu, espèce, genre...) et le niveau phylogénétique regroupant l’ensemble des individus étudiés.

Face à ces échelles, on peut se poser la question : “Les patrons de diversité sont-ils similaires à toutes les échelles spatiales et organisationnelles ? Quelles sont les implications en termes de règles d’assemblage ?”. C’est la question que j’aborde dans la partie 1, en interaction avec l’idée de varier les choix méthodologiques (4) en terme de modèle nul et de pool d’espèce.

Partie 2 : Décomposition α, β, γ des nombres de Hill - extensions méthodologiques

Ce chapitre s’intéresse exclusivement au point (4), c’est-à-dire aux perspectives qu’apporte la remise en cause des présupposés méthodologiques contenus dans le choix des indices de diversité. Comme mentionné précédemment, la littérature scientifique sur les indices de diversité est très (trop) riche, mais récemment de nombreuses unifications ont été proposées, notamment celles qui concernent la généralisation des nombres de Hill. À travers cela, la première partie se consacre à la remise en cause de la façon de prendre en compte le patron d’abondance des communautés et la façon d’évaluer la similarité écologique entre espèces à partir des données de traits fonctionnels et de la phylogénie. On peut se poser la question : “Les patrons de diversité sont-ils similaires selon le choix de l’indice de diversité ? Quelles sont les implications en termes de règles d’assemblage ?”

Partie 3 : Aspects méthodologiques de l’analyse des données de métabarcoding

Le méta-barcoding est en train de s’affirmer comme une nouvelle approche pour étudier les communautés [POISOT et collab., 2013; TABERLET et collab., 2012]. Elle amène des perspectives importantes pour l’étude de communautés qu’il est difficile d’échantillonner par des techniques classiques : bactéries, champignons ou archées. C’est en revanche un type de données assez différent des données de communautés traditionnelles

et qui présente de nombreux défis. Les données de méta-barcoding se caractérisent notamment par une assignation taxonomique partielle, ce qui, rejoignant le point (3) amène une perspective différente sur ce qu'est "une espèce" dans un échantillon de barcoding. Ce dernier chapitre comprend principalement des travaux préliminaires qui explorent les défis méthodologiques posées par le méta-barcoding dans le contexte de son utilisation pour étudier les patrons de diversité "taxonomique" et phylogénétique.

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Première partie

Diversité fonctionnelle des communautés végétales alpines et effets d'échelles

Introduction

Les effets d'échelles constituent une problématique discutée depuis longtemps en écologie [Chave, 2013; Levin, 1992]. Leur considération est critique lors de l'étude des communautés. Ces derniers sont potentiellement les résultats de l'interaction d'un grand nombre de processus déterministes et stochastiques opérant à des échelles différentes. Selon l'échelle à laquelle l'écologue analyse son système d'étude, certains processus écologiques seront plus susceptibles être détectés et étudiés.

Dans son essai sur la question, Wiens [1989] affirma que les résultats divergents entre les études scientifiques de systèmes similaires pouvaient provenir de ces effets d'échelle. En effet, la non-détection d'un processus dans une étude scientifique peut être seulement due à un mauvais choix d'échelle et non pas à son absence effective. En conséquence, il plaida en faveur d'une "science de l'échelle en écologie" pour permettre de mieux synthétiser les contradictions apparentes de notre discipline. L'étude des patrons de diversité ne fait exception [Vamosi et collab., 2009; Weiher et collab., 2011] et mieux prendre en compte les effets d'échelle en écologie reste une problématique qui est encore discutée [Chave, 2013; Thuiller et collab., 2010] et parfois explicitement étudiée [Carboni et collab., 2013; Chase et Myers, 2011; Swenson et collab., 2006].

Il existe de nombreuses échelles dont il est important de tenir compte en écologie. Au cours de ma thèse, je me suis concentré sur deux d'entre elles : l'échelle spatiale et l'échelle organisationnelle. Ensemble, elles définissent quatre caractéristiques du système analysé. Les deux premières se rapportent à la perspective spatiale de l'étude et les deux suivantes à sa perspective organisationnelle [Münkemüller et collab., 2014]. Le reste de cette introduction sera consacré à la définition de ces effets d'échelle et à exposer leur lien avec l'étude des patrons de diversité ; c'est-à-dire selon l'échelle de l'étude, les règles d'assemblage qui sont les plus prédominantes.

1 Échelle spatiale

1.1 Définitions

L'échelle spatiale de l'étude fait référence à (1) la surface de l'unité échantillonnée (communauté, site, paysage...) ou "grain", et (2) à la surface géographique contenant les communautés observées, ou "étendue". Par rapport à la méthodologie de l'étude des pa-

trons de diversité vue précédemment, l'étendue est souvent le pool d'espèces auquel les communautés sont comparées [GÖTZENBERGER et collab., 2012; WIENS, 1989]. Techniquement, ces deux dimensions ne sont pas indépendantes, la taille de grain étant nécessairement inférieure ou égale à l'étendue. Par ailleurs, dans le contexte de l'écologie des communautés, le grain doit nécessairement se comprendre comme relatif à l'espace utilisé par un individu, ce qui explique qu'une étude de communautés d'arbres aura une taille de grain plus grande (par exemple, 700 m^2 dans l'étude de KUNSTLER et collab. [2012]) qu'une étude de communautés mycorhiziennes où l'unité d'échantillonnage peut se réduire à un échantillon d'une racine (ex. TOJU et collab. [2014]).

Se référant tous deux à des surfaces spatiales, le grain et l'étendue spatiale se lient directement à la notion de la courbe aire-espèce. Elle est un des patrons les plus classiques en écologie : plus la surface géographique considérée est grande, plus la diversité biologique qui lui est associée sera grande [DRAKARE et collab., 2006; MAZEL et collab., 2014]. Les mécanismes écologiques sous-jacents à cette relation expliquent la dépendance spatiale des patrons de diversité.

Ainsi la diversité d'une zone définie sur une faible surface aura une diversité qui résulte de conditions abiotiques spécifiques, du résultat de processus biotiques qui auront exclu certaines espèces et favorisé la persistance d'autres, de contingences historiques qui auront fait que certaines espèces n'ont jamais eu l'opportunité de s'y implanter, d'un effet d'échantillonnage... Plus la surface de la zone grandit, moins l'hétérogénéité spatiale de la diversité associée à ces processus sera agrégée : les conditions abiotiques sont moins spécifiques car des gradients de plus en plus larges sont inclus dans la zone, la plupart des individus n'interagissent pas directement, l'effet d'échantillonnage devient moins prononcé...

1.2 Grain grossier et grande étendue ou "grande échelle spatiale"

Si l'étude s'appuie sur une grande aire géographique de référence (donc une grande "étendue"), par exemple, au hasard, une vallée alpine, la diversité biologique sera représentative de communautés réparties sur des gradients environnementaux importants et donc contiendra un grand nombre d'espèces, donc une plus grande variété de traits fonctionnels [STEIN et collab., 2014; WILLIS et collab., 2010] ou de lignées peu apparentés. Une communauté végétale peut être définie sur un grain grossier, par exemple à l'aide un relevé de Braun-Blanquet (cf. Chapitre 1) qui s'effectue une surface suffisante pour obtenir un échantillon représentatif de la végétation locale. Dans un tel cas de figure, on cherche délibérément à agréger certains effets très locaux (effet d'échantillonnage, effet de patch...).

Au final, la combinaison de ces deux entités paraît idéale pour détecter l'empreinte éventuelle des gradients environnementaux de la vallée car (1) les processus locaux se compensent au sein de la communauté rendant la communauté typique de "l'habitat

local" et le pool d'espèces, lui est représentatif de la diversité de gradients abiotiques importants [MOUQUET et collab., 2012; THUILLER et collab., 2010]. Ainsi il est probable que si une espèce est absente de la communauté ce soit en raison de conditions abiotiques défavorables.

On peut aussi travailler à des échelles plus grandes que celles d'une vallée, par exemple, en définissant une étendue à l'échelle de tout le massif alpin ou du biome. Dans ce cas là, le patron de diversité des communautés étudiées est étudiés dans une perspective plus biogéographiques étant donné que la déviation de sa composition peut être due à des contingences historiques ou macro-écologiques [CANTALAPIEDRA et collab., 2014].

2 Échelle organisationnelle

La perspective organisationnelle de l'étude se réfère au (1) niveau taxonomique auquel les individus sont identifiés et sont par la suite considérés comme identiques au sein de ces catégories ainsi qu'à (2) la profondeur phylogénétique, qu'ont en commun l'ensemble des individus étudiés. Classiquement les individus sont identifiés par rapport à l'espèce. En calquant la terminologie de l'échelle spatiale, on peut donc qualifier ces deux entités de, respectivement, "grain organisationnel" et "étendue organisationnelle".

2.1 Grain organisationnel

Classiquement, en analyse des patrons de diversité, le grain organisationnel est l'espèce. Ainsi la richesse taxonomique d'une communauté sera son nombre d'espèces, sa diversité phylogénétique sera quantifiée à partir d'une phylogénie résolue au niveau des espèces et sa diversité fonctionnelle sera quantifiée à partir des traits fonctionnels moyennés au niveau des espèces.

Prenant le contre-pied de cette supposition, BOLNICK et collab. [2003] plaida pour l'émergence d'une "écologie des individus" pour prendre en compte ces processus de plasticité ou d'adaptation potentiellement importants pour comprendre l'assemblage des communautés. Une littérature conséquente a depuis émergé en écologie fonctionnelle pour utiliser des données de traits prenant en compte la variabilité intraspécifique plutôt qu'en se basant sur des valeurs de traits moyennées au niveau de l'espèce [ALBERT et collab., 2010b; CIANCIARUSO et collab., 2009; JUNG et collab., 2010; MESSIER et collab., 2010]. Dans le cas de l'étude de la diversité fonctionnelle des communautés végétales, il a été montré que les espèces ne sont pas des entités homogènes et que leur variabilité phénotypique est un élément-clef de la définition de leur niche [ALBERT et collab., 2010a]. Cela est particulièrement vrai pour certains traits, en particulier ceux lié à la composition chimique des feuilles (LNC, LCC, δ^{13}C, δ^{15}N), qui ont souvent une forte variance intraspécifique et rendant son ignorance critique [KAZAKOU et collab., 2014]. L'étude de la variabilité intraspécifique est intéressante parce qu'elle permet potentiellement de révéler des pro-

cessus écologiques fins, tels que l'ajustement plastique ou adaptatif de caractéristiques phénotypiques en réponse à des modifications abiotiques [ALBERT et collab., 2010a] ou en réponse à des interactions biotiques [VIOLLE et collab., 2009a,b]. Plus pragmatiquement, ignorer la variabilité intraspécifique peut aussi tout simplement conduire à une mauvaise estimation de la diversité fonctionnelle et par conséquent fausser les résultats de l'analyse.

Dans le cadre des règles d'assemblage des communautés, VIOLLE et collab. [2012] proposèrent une réactualisation de la théorie des filtres d'assemblage incluant la variabilité intraspécifique ainsi qu'un cadre d'analyse statistique associé. Comme le notent ces auteurs, paradoxalement pour une discipline obsédée par les raisons de la coexistence entre espèces, l'écologie des communautés a longtemps ignoré la variabilité intraspécifique malgré le fait qu'un de ses travaux fondateurs [MACARTHUR et LEVINS, 1967] formalise la limitation de la similarité en s'appuyant sur la niche écologique des individus plutôt que sur celle des espèces. Différentes études ont depuis montré que l'inclusion peut changer sensiblement les résultats d'analyse des patrons de diversité fonctionnelle [JUNG et collab., 2010; KICHENIN et collab., 2013; SIEFERT, 2012].

À l'inverse, certaines études ont montré l'intérêt de grossir le grain organisationnel [MUNOZ et collab., 2014] permettant ainsi de révéler des règles d'assemblage se faisant au niveau des familles. Dans ce cas-là, le fait de considérer des familles entières homogènes en termes de niche peut permettre de se libérer du "bruit" que génère l'assemblage à des niveaux taxonomiques inférieurs. Un niveau taxonomique grossier peut être également subi, notamment dans les cas où l'identification des espèces est difficile. C'est le cas notamment du metabarcoding environnemental [TABERLET et collab., 2012; VALENTINI et collab., 2009], où l'unité "communauté" est redéfinie comme un ensemble de MOTUs (molecular operational taxonomic unit), présents dans un échantillon de sol par exemple, plutôt qu'un ensemble d'espèces, auxquelles on peut associer traits et relations phylogénétiques [PELLISSIER et collab., 2014; POISOT et collab., 2013].

2.2 Étendue organisationnelle

Elle est plus souvent qualifiée d'échelle phylogénétique ou taxonomique [CAVENDER-BARES et collab., 2006]. Comme évoquée dans l'introduction, l'étendue organisationnelle est inhérente à la définition de la communauté qui est souvent restreinte à une lignée phylogénétique bien définie [FAUTH et collab., 1996].

L'idée générale derrière la réduction de l'étendue organisationnelle ou phylogénétique est de restreindre le degré de dissimilarité entre les espèces étudiées. Une étude avec une petite étendue organisationnelle se restreindra à l'étude d'un ensemble d'espèces proches phylogénétiquement donc susceptibles de partager des caractéristiques écologiques similaires [CAVENDER-BARES et collab., 2009; CORNWELL et collab., 2014]. C'est pourquoi il a été suggéré qu'à petite étendue organisationnelle, il est plus aisé de

détecter l'impact des interactions biotiques, car elles sont théoriquement plus intenses entre proches parents, une hypothèse qui descend en droite lignée de l'hypothèse de naturalisation de DARWIN [1859]. Ainsi des études se sont attachées à décrypter les patrons de diversité à une étendue relative au genre [CAVENDER-BARES et collab., 2004] ou des familles [SLINGSBY et VERBOOM, 2006]. À l'inverse, une grande étendue phylogénétique prendra en compte des espèces très différentes avec des niches écologiques probablement différentes aussi. Il sera alors plus aisé de détecter l'influence de ce qui peut faciliter la détection des filtres biogéographiques, notamment parce que les adaptations liées à la niche bioclimatique tendent à être conservées phylogénétiquement [CRISP et collab., 2009].

3 Tirer parti des effets d'échelles

Si un niveau d'échelle particulier est plus approprié pour détecter certaines règles d'assemblage plutôt que d'autre, il devient alors pertinent de varier l'échelle d'une étude afin de détecter l'ensemble des règles d'assemblage affectant les communautés étudiées. Comme nous l'avons vu il est techniquement possible de varier les échelles spatiales et organisationnelles selon quatre axes partiellement indépendants (dans la mesure où la taille du grain reste inférieure à la taille de l'étendue), les études de CAVENDER-BARES et collab. [2006] et SWENSON et collab. [2006] sont à ce titre, parmi les plus complètes, car elles varient à la fois l'étendue spatiale et l'étendue phylogénétique et montrent comment les patrons de diversité phylogénétique suggèrent une limitation de la similarité lorsque les deux étendues sont petites. En revanche elles ignorent la question de l'impact des grains spatial et organisationnel.

Dans cette perspective, les communautés végétales alpines, en particulier leur diversité fonctionnelle, constituent un objet d'étude intéressant pour tester ces effets d'échelle. Ce sera l'objectif général de ce chapitre.

On peut faire l'hypothèse raisonnable que la règle d'assemblage principale qui affecte les communautés est le filtre généré par les gradients climatiques des Alpes. La théorie prédit que le filtre abiotique sera d'autant plus perceptible que le grain des communautés sera grossier et l'étendue grande, aussi bien d'un point de vue spatial qu'organisationnel. A partir de là, on peut se demander si à des grains et étendues plus fines, le patron de diversité révèle des règles d'assemblage locales auparavant dissimulées par le filtre abiotique, notamment des interactions biotiques [CHOLER et collab., 2001] ou si au contraire, localement, la composition des communautés végétales est essentiellement stochastique [MITCHELL et collab., 2009] voire un épiphénomène pour reprendre le terme de RICKLEFS [2008] peu informatif des règles d'assemblage des communautés. Cette question est l'objectif général de cette partie et de ses deux chapitres.

Le premier article de cette partie s'attache à étudier le patron de diversité fonction-

nelle de communautés végétales de la vallée de la Guisane dans les Alpes françaises définies sur des grains spatiaux et organisationnels grossiers (relevés de Braun-Blanquet et données de traits fonctionnels à l'échelle de l'espèce) en faisant varier l'étendue spatiale et organisationnelle de l'étude. Cet article s'attache à montrer l'intérêt de l'utilisation de modèles nuls contraints pour atteindre cet objectif [HARDY et SENTERRE, 2007; PERES-NETO et collab., 2001].

Le second article, en préparation, se consacre à l'étude du patron de diversité de vingt communautés végétales alpines échantillonnées à Valloire (Alpes françaises) dans le cadre de cette thèse. L'optique de cette étude est d'étudier l'influence des gradients environnementaux locaux sur leur diversité fonctionnelle tout en variant les deux composantes de l'échelle spatiale (grain et étendue) et le grain organisationnel (via l'ignorance ou non de la variabilité intraspécifique fonctionnelle).

Le troisième article dont je suis co-auteur, est une méta-analyse portant sur un jeu de données unique de 629 communautés et 36 traits fonctionnels étudiant l'importance de la variabilité intraspécifique au sein des communautés et entre communautés. Cette étude visait notamment à montrer les différences en traits fonctionnels et l'importance de l'échelle spatiale. J'ai participé à l'analyse statistique et à l'écriture de ce travail. L'abstract de cet article, maintenant soumis est en annexe.

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Chapitre 1

A family of null models to distinguish between environmental filtering and biotic interactions in functional diversity patterns

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SPECIAL FEATURE: FUNCTIONAL DIVERSITY

A family of null models to distinguish between environmental filtering and biotic interactions in functional diversity patterns

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Abstract

Questions: Traditional null models used to reveal assembly processes from functional diversity patterns are not tailored for comparing different spatial and evolutionary scales. In this study, we present and explore a family of null models that can help disentangling assembly processes at their appropriate scales and thereby elucidate the ecological drivers of community assembly.

Location: French Alps.

Methods: Our approach gradually constrains null models by: (1) filtering out species not able to survive in the regional conditions in order to reduce the spatial scale, and (2) shuffling species only within lineages of different ages to reduce the evolutionary scale of the analysis. We first tested and validated this approach using simulated communities. We then applied it to study the functional diversity patterns of the leaf–height–seed strategy of plant communities in the French Alps.

Results: Using simulations, we found that reducing the spatial scale correctly detected a signature of competition (functional divergence) even when environmental filtering produced an overlaying signal of functional convergence. However, constraining the evolutionary scale did not change the identified functional diversity patterns. In the case study of alpine plant communities, investigating scale effects revealed that environmental filtering had a strong influence at larger spatial and evolutionary scales and that neutral processes were more important at smaller scales. In contrast to the simulation study results, decreasing the evolutionary scale tended to increase patterns of functional divergence.

Conclusion: We argue that the traditional null model approach can only identify a single main process at a time and suggest to rather use a family of null models to disentangle intertwined assembly processes acting across spatial and evolutionary scales.

Introduction

The effect of biotic interactions on community structure has been predominantly studied at small spatial scales (e.g. Swenson et al. 2006), but new evidence suggests that this effect is also pervasive at large spatial scales (Gotelli et al. 2010). However, it is often difficult to detect signatures of biotic interactions in large-scale diversity patterns due to the overriding selective effect of abiotic processes (Vamosi et al. 2009).

Studies intending to infer processes of community assembly from diversity patterns often focus on niche dissimilarities between co-existing species (Kraft et al. 2007; Münkemüller et al. 2012). The level of species niche overlap in a community can be described via functional diversity indices using a set of functional traits, which reflect species' ecological characteristics (Lavorel & Garnier 2002). Under strong environmental filtering, successful species in a local habitat are more likely to share similar trait values leading to functional convergence

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(Petchey et al. 2007). Under strong competition, species with overlapping niches are less likely to co-exist leading to functional divergence (MacArthur & Levins 1967). Although theoretical predictions of functional diversity patterns are straightforward when assembly processes are considered in isolation, ecologists face difficulties in elucidating the opposing effects that biotic and abiotic processes have on patterns of functional diversity in communities when these two processes interact with each other.

The traditional approach to studying community assembly rules

The statistical approach to identify the signal of competition vs. environmental filtering is based on the idea that communities assemble through a hierarchy of ecological filters (Diamond 1975; Weiher & Keddy 1995). In the first stage of this hierarchical approach, a 'regional species pool' is defined as the set of species present in the region due to biogeographical and historical processes (Ricklefs 2004). Successive environmental factors (e.g. climate, land use or soil) filter adapted species from this 'regional pool' into a more convergent 'local species pool'. In a second stage, species from the local species pool are filtered by biotic interactions to form the 'observed communities'. When competition for resources predominates, we expect a pattern of functional divergence in the observed community relative to the local species pool.

The detection of significant patterns relies on comparing the observed functional diversity to the diversity expected under a model of random assembly from a selected species pool. Often patterns of competition can only be identified when comparing observed communities to random assemblies from the local species pool, because the regional species pool tends to be functionally too diverse. Therefore, the identification of an appropriate local species pool has been widely discussed but no consensus has yet been reached (Pärtel et al. 2011). Here, we propose to further constrain the traditional null model approach based on the regional pool composed of all species observed in the study (de Bello 2012). Our suggested constraints on this regional species pool take into account two important factors that are responsible for the differences between the regional and the local species pool: the spatial and evolutionary scales.

The effects of spatial and evolutionary scales

The spatial scale of a study can either relate to the extent of the sampling area across which the species pool has been constructed (e.g. habitat, region or continent) or to the resolution (i.e. plot size) of the study. Albeit potentially important, we do not investigate the effect of spatial resolution (Vamosi et al. 2009) in this study. Often a study with a large spatial scale includes a broad range of environmental conditions and thus a species pool with a broad range of trait values (Willis et al. 2010). Large scales thereby reinforce the detection of the effect of environmental gradients, while a small spatial scale is better suited to detect competition (Thuiller et al. 2010; Mouquet et al. 2012). The evolutionary scale is determined by the age of the lineages considered (e.g. which can delimit genera or families). We expect that it is more likely to detect environmental filtering when the evolutionary scale is large, because adaptations related to the bioclimatic niche tend to be conserved within old lineages (Crisp et al. 2009), which could mask the level of functional divergence expected between closely related competing species.

Studies exploring community patterns of functional diversity at both varying evolutionary and spatial scales are rare (e.g. Swenson et al. 2006). One interesting finding is that not only a too large spatial scale but sometimes also a too small spatial scale can hinder the detection of biotic interactions. This may happen because the species pool misses species for which the environmental conditions are suitable but which are excluded by competition from the entire study. This 'dark diversity' (*sensu* Pärtel et al. 2011) may be present in neighbouring areas or lie dormant in the soil seed bank. Including such dark diversity in the local species pool can be critical for detecting biotic interactions (de Bello et al. 2012b).

Here, we explore the interacting effects of gradually changing spatial and evolutionary scales of the species pool on patterns of functional diversity and inferred processes of community assembly. First, we present a simulation study using virtual community data generated with a process-based model that allows fine-tuning of the relative strengths of the different assembly processes present. Second, we present a field case study using plant community plots in the French Alps. We assume the patterns of functional diversity in alpine plant communities will be dominated by strong environmental filtering but biotic interactions are also likely to operate, although quite rarely discerned in such systems (e.g. Spasojevic & Suding 2012). The challenge is thus to remove the large-scale environmental filtering effects from the diversity patterns in order to detect the influence of small-scale processes. Finally, we propose a family of null models to distinguish the respective effects of environmental filtering and competition by manipulating the spatial and evolutionary scales in the statistical analyses, and test our proposed methodology with the virtual community data and the case study.

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Methods

Data

Simulation study – Model overview

In a first step, we generated 10 000 independent species pools of 400 species by simulating phylogenies and trait evolution along these phylogenies, with rates of trait evolution (δ) varying over evolutionary time (Pagel 1999). Each species was characterized by a single trait that defined the species-specific niche optimum and a niche breadth that was equal for all species. The phylogenetic signal for these traits, i.e. the trend for closely related species to be more similar than distantly related species, was measured using Blomberg's K (Blomberg et al. 2003).

For each species pool, a single community was initialized with 100 individuals randomly drawn from the species pool. For each simulation step, 100 random individuals were sequentially removed from the communities and replaced by individuals from the species pool (asynchronous updating). The probability of an individual from species i entering the community k, $P_{all,i,k}$, depended on the specified assembly rules and their relative importance defined by the factors B_{env} (environmental filtering), B_{comp} (competition) and B_{abun} (recruitment) (Table S1).

$$P_{all,i,k} = \exp\left(B_{env} \times \log\left(P_{env,i,k}\right) + B_{comp} \times \log\left(P_{comp,i,k}\right) + B_{abun} \times \log\left(P_{abun,i,k}\right)\right) \quad (1)$$

$P_{env,i,k}$ modelled the environmental filter: the closer the species trait value (i.e. niche optimum of the species) was to the environmental conditions of the community k, the higher was its probability to enter. $P_{comp,i,k}$ modelled the competition filter: the closer the species trait value was to those of the individuals already present, the lower was its probability of entering. In this way, competition between individuals was defined as symmetric. Note that as conspecifics had the same trait values, intra-specific competition was stronger than inter-specific competition. $P_{abun,i,k}$ modelled the recruitment filter: the more abundant the species was in the community, the higher its probability of entering. This term counteracted the high intra-specific competition value generated by the competition filter (see Appendix 1 for details on how the three filters were defined).

The factors B_{abun}, B_{env} and B_{comp} weighted the importance of the three filters in community assembly. In the special case of B_{env} and B_{comp} equalling one, the equation was comparable to a Lotka-Volterra equation with inter- and intra-specific competition and a maximal growth rate dependent on environmental suitability.

We repeated each of the 100 combinations of the parameters B_{env} (five values), B_{comp} (four values) and δ (five values; Table S1) 100 times, leading to a total of 10 000 simulated communities with different assembly rules and different phylogenetic contexts.

Field case study

Study system and site. The study site was the 25-km long Guisane Valley located in the centre of the French Alps (ca. 260 km^2; 44.9° N, 6.5° E). The valley was characterized by contrasting climate conditions, with mean annual temperatures ranging from −2.7 °C to 7.7 °C. As in other valleys of the central Alps, the landscape is a mosaic of coniferous and deciduous forests, shrub heaths, sub-alpine grasslands and alpine meadows. All these habitats were represented in our data set.

Community data and distribution data. We used two databases compiled by the Alpine National Botanic Conservatory. The data used to study community patterns were from a phytosociological survey at the scale of the French Alps, from which we extracted the 95 sites for the Guisane valley (Boulangeat et al. 2012b). Sites were representative of the heterogeneity of the valley climate conditions (Albert et al. 2010). Herbaceous community plots were surveyed by expert botanists in homogeneous vegetation with a size of 100 m^2 on average. Smaller plots had a minimum of 10 m^2 and some forest plots were sampled up to 1000 m^2. The abundance estimates were based on an abundance–dominance scale using cover classes (0.5, 3, 15, 37.5, 62.5 and 87.5%) and then normalized between 0 and 1 to obtain an estimate of the relative abundance of each species. Our community data set included 542 species. The second data set used to include dark diversity into our definition of species pools was a plant occurrences database (presence-only data) covering the French Alps (3 million occurrence points for 2748 species).

Functional traits. We used the functional trait database ANDROSACE (see Appendix 2 for details). We chose three functional traits: specific leaf area, height and seed mass to describe species' ecological strategies according to the leaf–height–seed scheme (LHS; Westoby 1998). These traits are strongly related to the fundamental processes of plant life, i.e. dispersal, establishment and persistence (Weiher et al.1999), and their combination has been proved to capture well the existing variation in plant ecological strategies (Lavergne et al. 2003). Specific leaf area (SLA, i.e. light intercepting area per leaf dry mass) reflects the trade-off between resource acquisition and conservation. Height at maturity is related to competitive ability and avoidance of environmental stress (Körner 2003). Seed mass strongly influences dispersal and is related to establishment ability (Pakeman et al. 2008). We calculated functional diversity on the basis of these three traits assuming that they capture essential aspects of the niche. Given this assumption, func-

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tional diversity of a community should be a good proxy for the amount of niche overlap in the community. In our study case, the three traits described above presented a low to moderate phylogenetic signal (K ranging from 0.08 to 0.44, see Table S2) and were linked to the main environmental gradient in the study area (see Fig. S2). Due to missing data in the trait database, we excluded 169 species characterized by less than two trait values. However, the remaining species still accounted for more than 80% of the total abundance of each community (Pakeman & Quested 2007). Finally, our data set represented a total of 95 communities and 373 species.

Phylogeny. A genus-level phylogeny of alpine plants was built using the workflow proposed in Roquet et al. (2013) with DNA sequences downloaded from Genbank (see Appendix 2 for details). The tips of the phylogenetic tree were resolved with polytomies to obtain a species-level phylogeny.

Statistical analyses

Functional diversity indices

We used Rao's quadratic diversity (Rao 1982), expressed as $D^{R} = \sum_{i} \sum_{j} d_{ij} f_i f_j$, with $d$ij being a measure of the functional distance between the species i and j, and fi being the relative abundance of species i in the community (Ricotta 2005).

For the simulated study, the functional distance between species was calculated as the Euclidean distance between their trait values. For the field study case, the three continuous traits were log-transformed to conform to normality and then standardized (i.e. centred and divided by their SD). The functional distance matrix was calculated for each species pool based on the Euclidean distances. We applied the R-function *quasieuclid* to ensure the Euclidean properties of our distance matrices despite the missing data (package *ade4;* Pavoine & Dolédec 2005; R Foundation for Statistical Computing, Vienna, AT).

Null model algorithms

Randomization schemes. The spatial scale of the null models could be adapted by randomizing either 'within the regional species pool' (large spatial scale) or 'within the local species pool' (small spatial scale). We thus decreased the spatial scale of the species pool by reducing it to the pool of species with similar environmental preferences to those conditions that prevailed within each community (as introduced by Peres-Neto et al. 2001). For each community, the randomization algorithm replaced each observed species with a species from the regional pool. In the 'suitability-based randomization' (SB-R), the probability of a species being selected depended on the probability of it occurring in the community given the environmental conditions ('suitability index'). In addition, we applied the 'equiprobable randomization' traditional approach (i.e. all species have an equal probability of being selected; EQ-R).

Similarly, evolutionary scale of the null models could be adapted by randomizing either 'across all lineages' (large evolutionary scale) or 'within lineages' (small evolutionary scale). We used the partial randomization scheme proposed in Hardy & Senterre (2007). For a given age, we defined the associated lineages across the phylogeny and only permuted the species within these lineages. This procedure could be repeated for several ages, thus making it possible to pinpoint shifting points of lineage age between convergent and divergent communities ('intra-lineages randomization', IL-R, vs. 'across-lineage randomization', AL-R, where the entire tree is randomized). We tested 19 age values regularly spaced along the tree. Note that IL-R could be easily combined with SB-R to study interacting effects of reduced spatial and evolutionary scales on functional diversity patterns (Table 1).

We analysed all simulated and real communities using these 40 different randomization schemes: one combining EQ-R and AL-R (non-constrained null model), one combining SB-R and AL-R, 19 combining EQ-R and IL-R, and 19 combining SB-R and IL-R.

Suitability indices. In order to perform SB-R, suitability indices were estimated for each species in each community. We defined suitability as a species' probability of occurring in the community given the environmental conditions. For each simulated community k and each species I, the suitability index was given as $P_{env,i,k}$ (Equation 1, Appendix 1).

For the field data, we built a species distribution model (Guisan & Thuiller 2005) in order to estimate species' abiotic niches, and thereby their probability of occurrence according to a set of climatic and topographic variables for each species independently (see Appendix 2 for details). Based on the species distribution models, we extracted the probability of presence (suitability indices) for the 373 plant species of the community data in each of the 95 communities.

Species pools. For the simulation study, the 'true' species pools were known and could be used directly for the different null models. For the field study, we constructed a *'Reduced species pool'* (R-SP) from the species present in the 95 community plots. We further construct an *'Extended species pool'* (E-SP) by adding 350 supplementary species (characterized by at least two trait values). These species were known to be present in the Guisane valley according to the plant occurrences database but were not present in our sampled community data set. The rationale behind this

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strategy was to include potential dark diversity, i.e. species able to both survive the environmental conditions of the Guisane and disperse into the communities under study (Table 1). Based on the species distribution models mentioned above, we extracted the probability of presence (suitability indices) for these 350 plant species in each of the 95 communities.

Outputs of null models

For each simulated community, we calculated the rank of the observed diversity value in the distribution of 500 randomized values of each of the null models. High (low) rank values indicated higher (lower) than expected diversity under the null expectation. We chose a significance level of 5% (0.025 and 0.975 significant threshold). We then studied the distribution of ranks across communities in relation to the parameters of the simulation model and the null models.

In the communities of the Guisane valley, the 40 different randomization schemes for each of the two species pools (R-SP, E-SP) resulted in a total of 80 null models. For each null model, we used 1000 repetitions and reported the ranks of observed values in the null distributions. We controlled for the size of the sample space for the evolutionary constrained null model, i.e. the number of possible random communities that could be generated by the null model. This was done for each evolutionary scale and each community.

The number of possible random communities r_{ij}, for a community i and an evolutionary scale j defining lineages L was calculated as: $\log(r_{ij}) = \sum_{L}\left[\log(n_L!) - \sum_{k}\log(n_{L,i,k}!)\right]$ with n_L the number of species in the lineage L and $n_{L,i,k}$, the number of species of the lineage L in the abundance class k of the community i.

All analyses were carried out using the software R 2.14, with the following packages: ade4, adephylo, ape, geiger, picante, spadicoR and randomForest.

Results

Simulation study

Influence of the suitability-based randomizations (spatial scale)

The null models built using both the traditional equi-probable randomization (EQ-R) and the suitability-based randomization (SB-R) correctly detected environmental filtering and competition processes when they acted in isolation (Fig. 1, upper right corner for competition, Benv = 0 and Bcomp = 10; and lower left corner for environmental filtering, Benv = 2 and Bcomp = 0). When the communities were randomly assembled (Benv = Bcomp = 0), EQ-R correctly detected neutral assembly (random diversity pattern), while SB-R wrongly indicated competition (significant divergence; Fig. 1, upper left corner). When both competition and environmental filtering were strong (Benv = 2 and Bcomp = 10), EQ-R was able to detect environmental filtering (significant convergence) but the additional use of SB-R also allowed detection of competition (Fig. 1, lower right corner); only when applied together did the two randomization schemes successfully disentangled the interplay of competition and environmental filtering. In the case of moderate environmental filtering (Benv = 0.5), EQ-R and SB-R successfully identified environmental filtering and competition if competition was also moderate (Bcomp = 1). When competition was stronger (Bcomp = 5), SB-R correctly identified competition but environmental filtering was too weak to be detected by EQ-R.

Influence of intra-lineage randomizations (evolutionary scale)

Overall, the intra-lineage randomizations (IL-R) did not better detect ecological processes than the across-lineage randomizations (AL-R). The median of the distribution of ranks was more or less constant regardless of the chosen age value for IL-R randomizations (Fig. 2, cutting at the root corresponds to AL-R) for all ecological processes.

The phylogenetic signal of trait distribution in the phylogeny only weakly influenced the outcome of IL-R and in an unexpected direction (Fig. 2). Even with a strong phylogenetic signal, the IL-R randomization scheme did not substantially increase the rank values (Table 2).

Field case study

For the restricted species pool (R-SP), a decrease of the spatial scale (i.e. use of SB-R, compared to EQ-R) only slightly shifted the ranks towards less convergent functional diversity patterns (mean rank increase of 0.09; Fig. 3, top left), showing that environmental filtering was less pervasive at smaller spatial scale, but still overwhelming. This trend was consistent across communities (98% of the communities ranks increased; Table 2).

For the sake of simplicity, we have only displayed the outcome of one IL-R null model and chose an intermediate evolutionary scale in Fig. 3 (roughly corresponding to lineages at the family or order taxonomic level). The reduction of evolutionary scales tended to increase the ranks but provided more variable results between communities than the reduction of spatial scale (Table 2). Finally, the combined reduction of spatial and evolutionary scales (using both SB-R and IL-R) most strongly increased the ranks (mean rank increase of 0.16; Fig. 3). Fifteen out of the 18 communities presenting a significant environmental filter-

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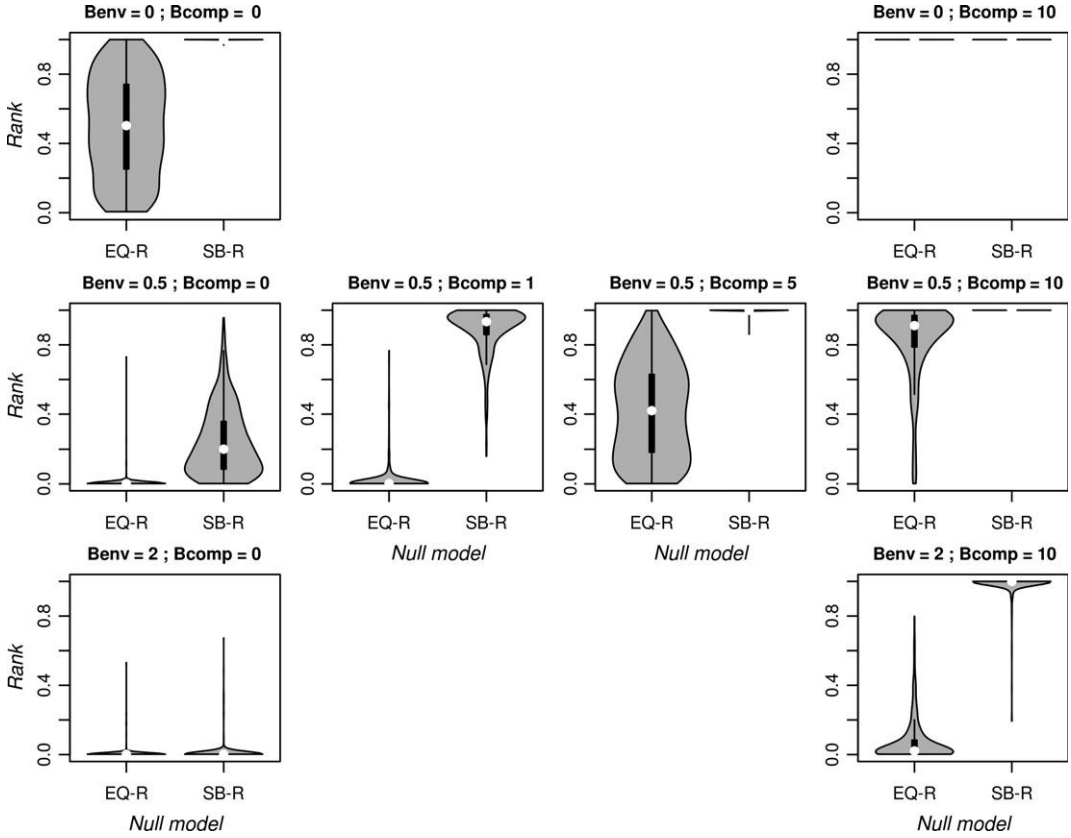

Fig. 1. Comparison of the outcomes of the 'equiprobable randomisation' (EQ-R) and the 'suitability-based randomisation' (SB-R) null models for the simulated community data. Each subplot presents the distribution of the ranks in a violin plot (Hintze & Nelson 1998) generated for a specific combination of environmental filtering (Benv) and competition (Bcomp). Community assembly is random in the upper-left corner, driven by competition only in the upper-right corner (Bcomp > 0), driven by environmental filtering only in the lower-left corner (Benv > 0), and driven by the interplay of these processes in the lower-right corner). A rank value higher than 0.975 indicates a diversity value higher than expected under the null model, while a rank value lower than 0.025 indicate a diversity value lower than expected under the null model

ing signal (convergence) at large spatial and evolutionary scale (EQ-R: AL-R) presented no signal (neutral pattern) at a small spatial and evolutionary scale (SB-R: IL-R).

For the extended species pool, we observed the same trends: the ranks obtained using the combination of SB-R and IL-R increased strongly compared to the use of a non-constrained null model (91% of the communities ranks increased; Table 2), showing that environmental filtering was less pervasive at the small rather than the large spatial and evolutionary scale. Moreover, 22 out of the 28 communities with a significant environmental filtering signal at large spatial and evolutionary scale (EQ-R: AL-R) showed no signal at a small spatial and evolutionary scale (SB-R: IL-R).

With an increasingly smaller evolutionary scale, the outcome of the null models (either EQ-R: IC or IL-R: SB-R) tended to detect a less convergent diversity pattern (i.e. the mean rank value increased; Fig. S4). This showed that the trend described above for a constraint on an intermediate evolutionary scale can be generalized: when the evolutionary scale was smaller, the environmental filtering was less pervasive, although the proportion of communities becoming significantly divergent remains negligible. This was true whatever species pool was considered. Furthermore, we note that the choice of cutting age for IL-R heavily impacted the sample space of the null model. At the chosen intermediate and larger evolutionary scale, the number of possible random communities remained largely superior to the number of used randomizations. However, for smaller evolutionary scales, the sample space of the null model decrease dramatically for some communities, indicating lower power of the null model.

Finally, regardless of the evolutionary and spatial scale considered, the communities appeared more convergent (i.e. ranks decreased; Fig. S3) when using the extended species pool (E-SP) as opposed to the reduced species pool

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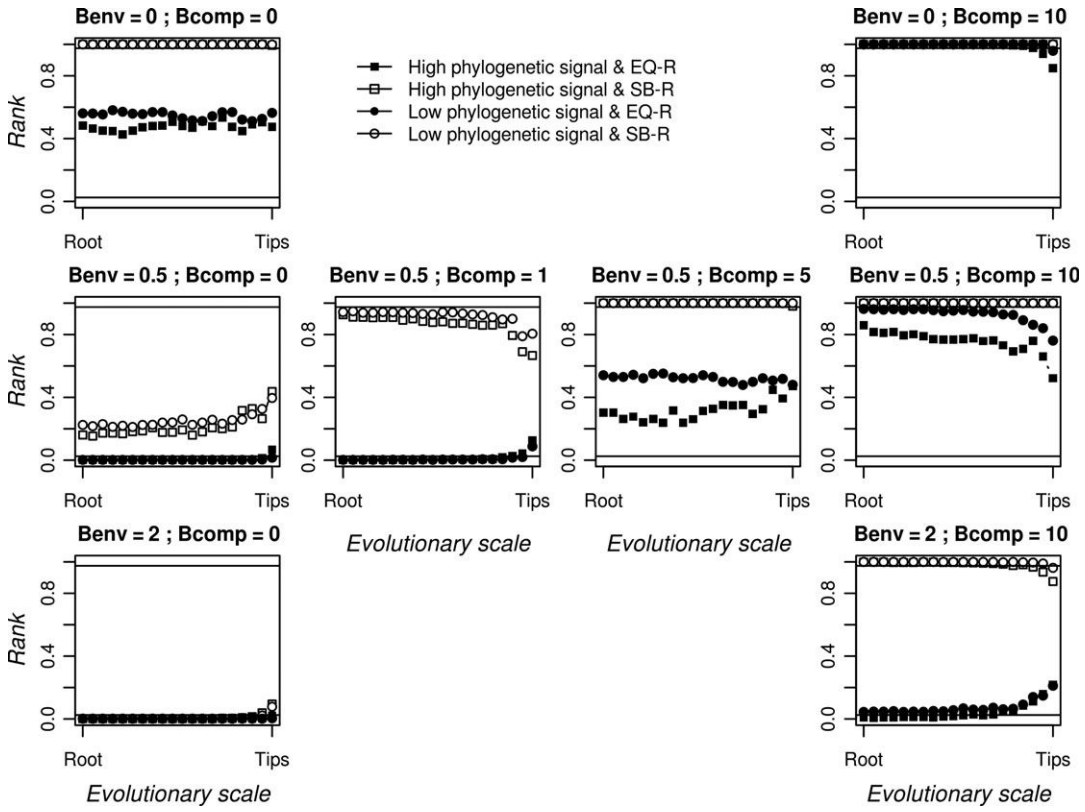

Fig. 2. Comparisons of the outcomes of the 'intra-lineages randomisation' (IL-R) as functions of the evolutionary scale. Each subplot contains the median of the distribution of ranks of communities generated for a specific combination of environmental filtering (Benv > 0) and competition (Bcomp > 0). A rank value close to 'Root' indicates a 'close-to-root' age value while an age value close to 'Tips' indicates a 'close-to-tips' age value. Specifically the randomizations at age 'Root' are 'across-clades randomisation' (AC-R), i.e. all tips are shuffled among each other. Closed (open) symbols indicates the coupling with EQ-R (SB-R); square (circle) symbols indicate the distribution of ranks for communities whose phylogeny was generated by a δ parameter of 0.1 (10) and thus high (low) phylogenetic signal.

(R-SP); however, the differences between these species pools were small.

Discussion

Detecting biotic interactions: scale matters

A primary result of our simulation study was that null models constraining the spatial scale help in detecting biotic interactions, even if these were overlaid with strong environmental filtering. These constrained null models reflected well the 'local species pool' (Zobel 1997). In contrast, reducing the evolutionary scale using intra-lineage randomization did not improve the detection of biotic interactions, even when the niche phylogenetic signal was high. The field case study provided complementary insights. The combined use of constraints for the spatial (SB-R) and the evolutionary (IL-R) scale increased divergence in the functional diversity pattern and thus identified a potential effect of competition. The inconsistency between the field and simulation studies about the importance of evolutionary scaling likely resulted from the fact that in the simulation study species niches were fully known and described by the functional patterns. The evolutionary scaling did not add any further information. In the field case study, the phylogenetic relationships were likely to capture species' niche dimensions not well represented by the measured traits, such as the nitrogen fixing ability of Fabaceae species. If measured traits do not fully represent species' niches, evolutionary constrained null models can be beneficial as they can buffer the lack of information on niche-relevant species traits in the functional analysis (Carboni et al. 2013).

Interpretation of diversity patterns from field data

Alpine communities are highly constrained by steep climate gradients (in particular temperature and radiation; de Bello et al. 2012a). The challenge is thus to go beyond

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Table 1. Overview of the different null models with null hypotheses associated with their tests.

	Name	Description	Associated Hypothesis	References
Randomization				
Large scale	Across-lineages randomization (AL-R)	Species abundance values are shuffled across the entire phylogeny	All species in the phylogeny are functionally equivalent	
Reduction of evolutionary scale	Intra-lineages randomization (IL - R)	Species abundance values are shuffled within pre-defined lineages (defined by age)	Species within lineages are functionally equivalent	Hardy & Senterre 2007
Large scale	Equi-probable randomization (EQ - R)*	Probability of being attributed to an abundance value is equal for all species	All species of the regional species pool are functionally equivalent	
Reduction of spatial scale	Suitability-based randomization (SB - R)	Probability of a species being attributed to an abundance value is proportional to the abiotic suitability of the site considered	Species of the local species pool are functionally equivalent	Peres-Neto et al. 2001
Species pools				
	Reduced species pool (R – SP)	Species pool composed of the species present in at least one of sites studied	The species in the data set fully describe the species pool	
	Geographical extended species pool (GE – SP)	Species pool extended to species present in the study area according to independent data	Dark diversity is missing and needs to be included in the species pool	Pärtel et al. 2011

*If evolutionary scales and spatial scales are independently varied, AL-R equals EQ-R. However, as they can be varied in combination (cf. Fig. 3, last column), we need to differentiate between AL-R and EQ-R.

Table 2. Summary of the change in ranks for the communities of the field case study when reducing spatial and evolutionary scales: at small spatial scale and large evolutionary scale (SB-R), at large spatial and small evolutionary scale (IL-R) and at small spatial and evolutionary scales (SB-R: IL-R). The reduced species pool (R-SP, first three rows) and the extended species pool (E-SP, last three rows). We used a 5% error rate to establish the significance threshold for switching ranks (0.025 and 0.975). For a graphical representation, see Fig 3.

	Percentage of communities increasing rank	Mean increase in rank	SD of rank increase	Number of communities switching from convergent to non-convergent	Number of communities switching from non-convergent to convergent/total number of communities
R-SP					
EQ-R to SB-R	98%	0.09	0.06	9/18	0/77
EQ-R to IL-R	79%	0.08	0.13	7/18	1/77
EQ-R to SB-R: IL-R	89%	0.16	0.16	15/18	0/77
E-SP					
EQ-R to SB-R	100%	0.12	0.09	18/28	0/67
EQ-R to IL-R	80%	0.07	0.11	14/28	2/67
EQ-R to SB-R: IL-R	91%	0.19	0.18	22/28	1/67

environmental filtering to detect the additional influence of small-scale processes on community assembly. It was thus logical to observe environmental filtering as the dominant assembly process when an equi-probable null model approach was applied (EQ-R). Reducing the spatial scale of the analysis by adding habitat suitability constraints (SB-R) reduced functional convergence, indicating that the environmental factors considered in the suitability index were originally driving the patterns of convergence. The functional convergence remaining might be due to further small-scale processes (e.g. micro-environmental conditions not included in the suitability index or other biotic interactions favouring the co-existence of similar species). Overall, we did not detect significant functional divergence in alpine plant communities, at any studied evolutionary or spatial scale. This result may have several explanations.

First, competitive interactions between plant species do not necessarily lead to trait divergence (e.g. Laliberté et al. 2013). Besides niche differentiation, the sharing of com-

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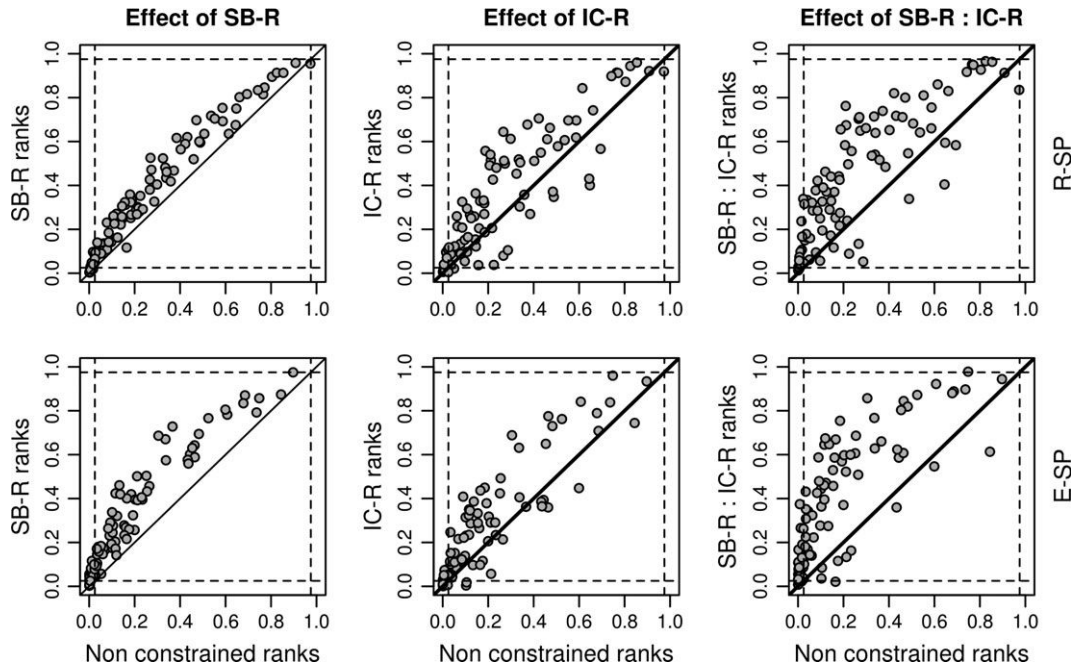

Fig. 3. Comparison of the outcomes of the different constrained null models for the case study according to the scales of the analysis. Results at large spatial and evolutionary scales (EQ-R: AC-R) are compared against the results: at fine spatial scale and large evolutionary scale (SB-R, first column), at large spatial scales and small evolutionary (IL-R, second column), and at fine spatial and evolutionary scales (SB-R: IL-R, third column). The first row presents results for the reduced species pool (R-SP) and the second row presents results for the extended species pool (E-SP). The dotted lines represent the significance threshold of the rank values (0.025 and 0.975). The thick lines separate the communities whose ranks increased from these whose ranks decreased with the use of the constrained null model vs. the non-constrained null model. For a numerical summary, see Table 2

mon traits that enhance competitive ability can also lead to the co-existence of species (Mayfield & Levine 2010). Second, our selection of key traits might not be appropriate to evaluate niche overlap. This is somehow unlikely, given that the use of these functional traits have been widely advocated for herbaceous ecosystems (Grime 2006). However, we neglect the intra-specific trait variability along the gradients of the Guisane valley (Albert et al. 2010). As competition is essentially an individual-level process, the use of aggregated species-level trait values could mask the functional divergence between competing neighbours (Clark et al. 2011). Third, other biotic interactions and local ecological processes, such as the removal of palatable species by grazers (de Bello et al. 2006) or local land use such as fertilization selecting for species with high SLA (Quétier et al. 2007; Gerhold et al. 2013), might influence diversity patterns towards convergence.

Overall, we conclude that characterizing species by their position in the LHS plant ecology strategy scheme mainly revealed the effect of environmental filtering at large spatial and evolutionary scales. Neutral processes and not niche-based competition seemed to drive community assembly at small spatial and evolutionary scales. These results are congruent with other studies suggesting that biotic interactions do not play an important role in the functional structuring of sub-arctic–alpine communities (Mitchell et al. 2009; but see Spasojevic & Suding 2012).

Detecting biotic interactions: (not) a matter of species pool

In our field case study, extending the species pool did not have a marked effect on the detection of competition. This result suggests that the analysis was robust to the inclusion of dark diversity. However, we cannot be sure that all of the dark diversity was included, as local competition could have excluded species from the entire Guisane valley.

Constraining species pools allows a reduction of the evolutionary scale but also increases the risk of Type II errors as less random combinations of species can be drawn from the species pool to construct the null expectation of the diversity pattern (Gotelli & Ulrich 2012). In our study, the effect of this risk is striking when using IL-R, as the sample space significantly decreases when the cutting age becomes very close to the tips (Fig. 4). When using IL-R, the sample space should therefore be evaluated beforehand to evaluate the power of the null model.

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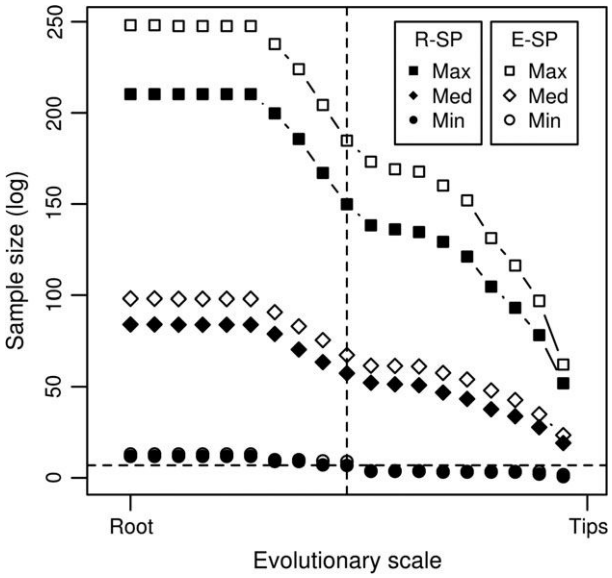

Fig. 4. Sample space of 'intra-lineage randomization' (IL-R) as a function of the evolutionary scale. Sample space was estimated as the number of different random communities the IL-R null model can generate for an 'observed' community and at varying evolutionary scales. We displayed the median (diamond), maximum (square) and minimum (circle) over communities for each species pool (R-SP, filled symbols; E-SP, open symbols). The horizontal dotted line indicates the threshold of 1000 random possibilities. The *x*-axis represents the age value used as a parameter for the IL-R and the vertical dotted line indicates the evolutionary scale used to generate Fig. 3.

Species distribution models as a new tool for diversity pattern analysis

Our study highlights the potential of species distribution models to refine the species pool concept by defining a pool of species adapted to local environmental conditions based on suitability estimates (introduced in Boulangeat et al. 2012a). One potential drawback is that suitability-based randomization (SB-R) might lead to false positives when using flawed suitability information. This situation occurred in our simulation study, where the species suitability indices were based on a trait unrelated to species' niches in the random community assembly scenario. As a result, the test wrongly identified divergence and thus competition as a major assembly process. This result calls for caution in real-life situations where the habitat zsuitability is assessed from the observed distribution of species, and may reflect other processes than environmental filtering. Such an approach should then be preceded by a cautious selection of relevant abiotic variables driving species distributions, niche differentiation and thus environmental filtering.

Perspectives for diversity pattern analyses

Detecting the influence of biotic interactions in observed diversity patterns is a challenging task because of the pervasive environmental heterogeneity in large-scale ecological data sets (Cavender-Bares et al. 2009; Thuiller et al. 2010). Using a family of null models allows changing of the spatial and evolutionary scales of the analysis. Caution should however be taken: we showed the negative impact of flawed input data on the output of constrained null models and the importance of evaluating the sampling space when constraining null models. Finally, the combined interpretation of the different null model outcomes enables uncovering of fine-scale functional divergence patterns within large-scale convergence patterns.

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Supporting information

Additional supporting information may be found in the online version of this article:

Appendix S1. Simulation model details.

Appendix S2. Field data details (phylogeny, trait database).

Figure S1. Simulation model illustration.

Figure S2. Relationships between the field case study functional traits and the environment.

Figure S3. Comparison of null models outcome between R-SP and GE-SP.

Figure S4. Influence of varying age values on IL-R outcome on the field data.

Figures S5–7. Complementary analyses on IL-R outcome on the field data.

Table S1. Simulation model parameters.

Table S2. Phylogenetic signal of the field case study functional traits.

Table S3. Phylogeny branch length calibration data.

Table S4. Summary of the comparison of null models outcome between R-SP and GE-SP.

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Chapitre 2

Spatial scale and intraspecific variability mediate the response of grassland trait diversity to alpine gradients

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1 Introduction

The importance of scale, especially spatial scales and organizational levels, is a long standing issues in ecology [CAVENDER-BARES et collab., 2006; CHAVE, 2013; LEVIN, 1992; MÜNKEMÜLLER et collab., 2014]. It has since been recognized as an important element in the assembly of communities [CARBONI et collab., 2013; VAMOSI et collab., 2009; WEIHER et collab., 2011] since different ecological processes are likely to play at different scales and thus generate scale-dependent diversity patterns. When studying the structure of tropical forests across spatial and taxonomic scales, SWENSON et collab. [2006] highlighted the "promise" of studying diversity patterns in order to disentangle the various processes that are likely to shape the assembly of local communities. While evaluating the change in species' identities and relative abundances across communities has a long tradition in community ecology [CODY et DIAMOND, 1975], recent work has highlighted the value of studying the change in functional distances among individuals, in order to identify the link between ecological processes and the phenotypical features of individuals. In terms of organizational levels, this means that we look at a finer resolution by not aggregating individuals within species. Functional distances are based on species' functional traits, i.e. measurable morphological, physiological or phenological features that impact their fitness via their effects on growth, reproduction, and survival in given environments [VIOLLE et collab., 2007]. Functional traits are directly connected to species' niches and affect how species are distributed along environmental gradients, and coexist locally in particular habitats [THUILLER et collab., 2010, 2004]. The study of community functional α-diversity, which measures the trait dispersion within communities and functional β-diversity, which measures the trait turnover between communities, has thus allowed ecologists to better understand the assembly rules shaping meta-communities [SPASOJEVIC et collab., 2014; THUILLER et collab., 2014; WEINSTEIN et collab., 2014]. The identification of significant patterns of α and β-diversity relies on comparing the observed functional diversity to the diversity expected under a null model of random assembly from a selected species pool [HARDY, 2008]. This species pool is usually a "regional species pool" defined as the set of species present in the region due to biogeographical and historical processes [RICKLEFS, 2004]. Here again, the relevant assembly processes, and thus the emerging patterns of functional α and β-diversities in comparison to null models, are highly dependent on focal scales, such as spatial scale and organizational levels [MÜNKEMÜLLER et collab., 2014].

Spatial scale has two important components : (1) the grain, or community area, that is the size of the sampling unit and (2) the extent, or the geographical area of the study, that defines the species pool to which the community structure is compared. At a fine grain, we may be more likely to detect assembly rules linked to biotic interactions as the study focuses on individuals that are close enough to interact directly while at a coarse grain, local processes (such as biotic interactions, local abiotic filtering...) are then averaged out

and become more representative of the impact of large-scale abiotic gradients.

Often a study with a large spatial extent includes a broad range of environmental conditions and thus a species pool with a broad range of trait values, while a small spatial extent reflects the local pool that groups species or individuals possessing suitable traits to survive local abiotic conditions [DE BELLO et collab., 2012]. A large study scale (aka. coarse grain and large spatial extent) should thereby reinforce the detection of climatic gradients' effects on community assembly, while a small spatial scale (aka. fine grain and small spatial extent) is often better suited to detect biotic interactions [WEIHER et collab., 2011] and small-scale environmental heterogeneity. That is why both spatial grain and extent have been argued to be important for the detection of assembly processes [VAMOSI et collab., 2009; WIENS, 1989] although they have been rarely studied simultaneously.

In functional trait studies, the organizational level often translates into the resolution at which phenotypic divergence is studied. Commonly, species are considered to be functionally homogenous entities, assuming that intraspecific trait variability (ITV) is negligible. However, in the recent years, numerous authors have shown that this assumption is disputable and that ITV can affect functional diversity [ALBERT et collab., 2012; SIEFERT, 2012]. Consequently, ITV is today more commonly integrated in biodiversity studies [JUNG et collab., 2010; KICHENIN et collab., 2013]. However, although hypotheses have been articulated [ALBERT et collab., 2011], the importance of ITV for detecting the signal of assembly rules relative to different spatial scales has rarely beentested to date (but see SIEFERT et collab. [2014]).

Here, we investigated the functional structure of twenty subalpine and alpine plant communities along an elevation gradient taking into account spatial scale (grain and extent) and intraspecific trait variability. We tested three hypotheses : (1) At large spatial extent and grain, plant community functional α-diversity responds primarily to climatic stress. We expect that the effect of landscape scale filters such as climatic stress should be pervasive at large spatial scale, and cause communities to appear functionally convergent (i.e. co-occurring individuals are more similar than expected under random assembly). (2) At small spatial extent and grain, functional α-diversity is shaped to a greater degree by biotic interactions. According to the *"stress-gradient hypothesis"* [CALLAWAY et collab., 2002; CHOLER et collab., 2001], we expect communities at the lower end of the climatic stress gradient to be structured by competitive interactions and, at the higher end, by facilitation. In terms of functional traits, competition at the lower end of the stress gradient can either result in limiting similarity and thus functional divergence or in competition hierarchies and thus functional convergence [MAYFIELD et LEVINE, 2010]. At the high end of the gradient, facilitation should lead to functional divergence because individuals with traits that are poorly suited to local abiotic conditions are locally facilitated by individuals with contrasting adaptive traits [GROSS et collab., 2013, 2009]. (3) The inclusion of ITV is more relevant at a small spatial grain and extent where species turnover is less pervasive than at a large spatial extent and grain. Moreover, it is expected that trait variance will

be greater at the inter-specific scale, thus the inclusion of a more diverse species pool will override the effect of intra-specific variability on observed patterns of functional diversity.

2 Methods

2.1 Study site

The study was conducted in the central French Alps (45.12°N, 6.40°E). (Figure 2.1). Ten sites were studied along a continuous 975 m elevation gradient (1750 - 2725 m) in a cow-grazed pasture. Subalpine grasslands dominated at the bottom of the gradient while upper elevations were characterized by sparsely vegetated alpine meadows.

The ten sites were evenly distributed along an elevation gradient, and were all situated on the same south-facing slope. The purpose of this design was to set all sites on a single large-scale stress gradient that encompassed two major alpine gradients : temperature and radiation [DE BELLO et collab., 2013]. In each site, we set up two square and non-overlapping plots of 100 m^2 . Within each plot, we studied plant communities at four grain sizes (see below). Overall, we thus collected data for 80 communities situated in 20 plots,which were nested in 10 sites (Figure 2.1).

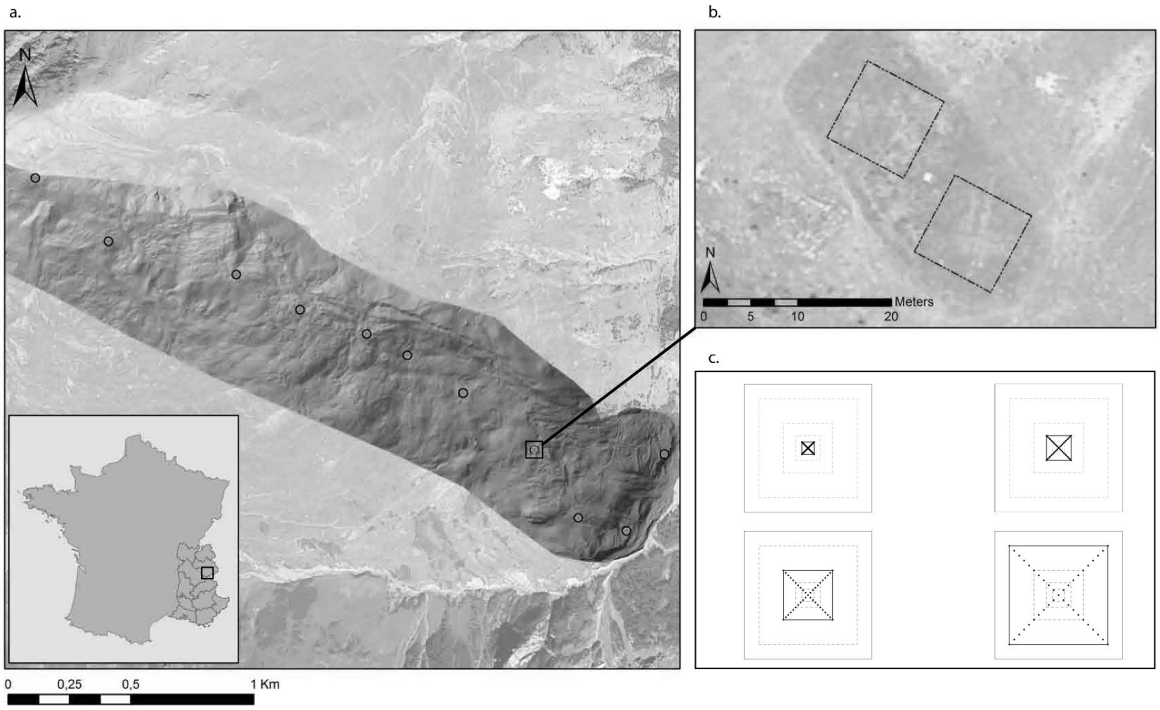

FIGURE 2.1 – Overview of the whole study area. a) Landscape scale, where dots indicate the position of the sites. b) Site containing two 10x10m plots. c) Within plots, black points show the positions of the sampled plant individuals according to the grain size : 1.25 by 1.25 m (upper left corner) ; 2.5 by 2.5 m (upper right corner) ; 5 by 5 m (bottom left corner) ; 10 by 10 m (bottom right corner).

2.2 Data

Nested sampling design

In each of the two plots located within the ten sites, we sampled plant individuals during peak productivity (ca. Mid-July 2012), along two transects set on the diagonals of each plot. The sampling protocol was designed in such a way that for each plot, we sampled four nested communities at four nested grain sizes. To sample the plot community at the coarsest grain (10x10m), we sampled a total of 41 plant individuals every 70 cm on each diagonal (20 on each one of them plus one at the center). We repeated the same protocol at the 5 by 5 m scale (41 individuals sampled every 35 cm), 2.5 by 2.5 m (41 individuals sampled every 17.5 cm) and 1.25 by 1.25 m (41 individuals sampled every 8.75 cm) along the same transects (Figure 2.1, (c)). Due to the sampling protocol, the four nested communities were partially characterized by the same set of individuals : two communities from the same plot at consecutive spatial scales thus shared half of sampled individuals. This allowed us to considerably reduce the sampling effort while keeping the sampling effort devoted to each community consistent. In total, 2020 individuals were sampled.

Functional traits

Each sampled individual was identified and seven functional traits were measured [CORNELISSEN et collab., 2003]. (1) Maximum vegetative height is the distance between the highest photosynthetic organ and the ground, which is associated with plant competitive vigor and tends to be allometrically correlated with above-ground biomass. (2) specific leaf area (SLA) is the one-sided area of a fresh leaf divided by its oven-dry mass ; SLA is usually well correlated with relative growth rate for herbaceous species [WESTOBY, 1998]. (3) Leaf dry matter content (LDMC) is the oven-dried mass of a leaf divided by its water-saturated fresh mass ; it was measured using the partial rehydration method, which has been proved to give results similar to the full rehydration method [VAIERETTI et collab., 2007] ; LDMC is related to the average density of leaf tissues and tends to scale negatively with SLA. (4) Leaf nitrogen concentration (LNC) is the total amount of nitrogen per unit of dry leaf mass, which quantifies the allocation of available nitrogen to photosynthetic enzymes in leaf chloroplasts [PÉREZ-RAMOS et collab., 2012; REICH et collab., 1999]. (5) Leaf carbon concentration (LCC) is the total amount of carbon per unit of leaf dry mass and represents investment in structural tissues [POORTER et BERGKOTTE, 1992]. (6) Leaf carbon isotopic ratio (δ^{13}C) provides a time-integrated measure of intrinsic water use efficiency and thus resistance to drought [PÉREZ-RAMOS et collab., 2012]. (vii) Leaf nitrogen isotopic ratio (δ^{15}N) provides a measure of the plant nitrogen acquisition strategy [GUBSCH et collab., 2011].

For LNC, LCC, δ^{13}C and δ^{15}N, dried and marble-ground leaves samples of 1-2 mg were analysed with a FlashEA 1112 elemental analyser (Thermo Fisher Scientific Inc., Milan, Italy) at the individual level.

Environmental variables

We collected a set of pseudo-bioclimatic variables relevant to understanding community structure and functioning in alpine environments. Climatic and topographical variables were sampled at the site level while soil variables were sampled at the plot level (Table 2.1).

1. In each site, we set up local weather station that recorded soil temperature with five captors at two depths (15 cm-25cm). Soil temperature was recorded over the course of at least a single year in each site (June 2012- October 2013) with a temperature measurement every hour. Yearly soil temperature was then evaluated by averaging soil temperature across the year and across captors. Because one station failed, we had missing data for the 8^{th} site (elevation 2450 m).
2. In alpine ecosystems, variation in snow cover duration along elevation and meso-topographic gradients is a key driver of plant distribution and community composition [CHOLER, 2005; EVANS et collab., 1989]. To account for this parameter, we estimated growing season energy budgets, as mediated by snowmelt dynamics area using a remote sensing-based snow distribution model [CARLSON et collab., 2015]. For five years falling between 2000 and 2014, daily maps of snow cover were used to estimate snow-free growing season days (daily mean air temperature >0°C) and snow-free frost days (daily mean air temperature > 0°C). Snow-free growing season length and the number of frost days were averaged across years and extracted for the studied sites.
3. Topographic variables were generated using 15cm LiDAR imagery that was acquired during the same year of the sampling (summer 2012). From this 15cm LiDAR image, we derived two fine-scale topographic layers of the area : (1) topographic wetness index (TWI), that is commonly used to quantify topographic control on hydrological processes. The index is a function of both the slope and the upstream contributing area per unit width orthogonal to the flow direction. (2) slope was estimated from the LiDAR imageries and averaged for each 10 by 10m plot of the sites.
4. In september 2012, at each plot, 6 composite soil samples (approximately 200-gr fresh weight) were sampled in plastic bags. All 120 samples were then stored at 4°C in a cooler in the field prior laboratory analyses which occurred within 24 hours. Soil bulk density and total porosity were estimated by measuring the dry mass of the soil core volume (app. 196.25-cm^3). Fresh soil subsamples were sieved at 5.6-mm, weighed and stored at 4°C. Soil water content (SWC) was determined from fresh soil dried at 105°C for one week [ROBERTSON et collab., 1999]. Subsequently, soil organic matter content (SOM) was measured by loss on ignition of the previously dried soils. Soil subsamples were air-dried and ground to estimate total soil C and N content using a Flash EA1112 (Thermo Fischer Scientific Inc.,Waltham, MA, USA). Soil pH was measured on fresh soil using a 1 :4 (soil : distilled water) solution.

Soil nutrients (ammonium (NH_4^+-N), nitrate (NO_3^--N), and total dissolved nitrogen (TDN), were measured colorimetrically from 0.5 M K_2SO_4 fresh soil extracts using standard protocols with a FS-IV colorimetric chain (OI-Analytical Corp., College Station, TX, USA). Potential nitrogen mineralisation (PNM) rates were estimated by incubating fresh soil subsamples (dark, 7 days, 40°C) under anaerobic conditions allowing organic N to be mineralized and accumulated as NH_4^+-N (Wienhold 2007). The difference between NH_4^+ content before (t1) and after the incubation (t2) gave PNM = [$(NH_4^+\text{-N})_{t2}$ - $(NH_4^+\text{-N})_{t1}$]/soil dry weight/7 days. Finally soil microbial biomass N was measured using the chloroform-extraction fumigation technique on fresh soil subsamples [VANCE et collab., 1987].

2.3 Analysis

Environmental gradients

We performed a principal component analysis (PCA) on the scaled environmental variables. The missing value for the yearly mean temperature of the 8th site was replaced with the mean of the variable across all sites. The PCA allowed us to identify three independent underlying gradients. Relationships between main PCA axes and abiotic variables are displayed in Table 2.1. The first axis was strongly related to elevation (cor = 0.93 ; $p < 0.001$) and represented 40% of the variance ; it was linked to decreasing annual mean soil temperature, growing season length, number of frost days, TWI, nitrogen stocks and flux. The second one was linked to soil composition and opposed mid-altitude plots with soil rich in organic matter, high total nitrogen content and high C :N ratio (negative scores along the 2nd PCA axis) to low and high altitude plots (positive scores), probably because of high decomposition rate at low altitude and important erosion at high altitude. Finally the third one was positively linked to the concentration of dissolved forms of inorganic nitrogen (ammonium and nitrate) and negatively to yearly soil temperature and had no obvious relationship with elevation. Because of this, we associated it to a consequence of topographic variation that generated a local temperature gradient, the persistence of inorganic nitrogen in the cold end of that gradient may thus be due to slower soil nitrogen cycling. Both the climatic and local temperature gradient were associated with decreased dry biomass production (data not shown).

We used these three gradients in the rest of the analyses and interpreted them as follows : (1) a gradient of climatic stress, (2) a gradient of soil parameters, (3) a local temperature gradient probably due to mesotopography.

Diversity indices

To calculate the functional α-diversity of each community with and without accounting for intraspecific variability, we first calculated the functional distance matrix between all sampled individuals. To do so, each functional trait was scaled. Since the functional

Name	Source	Resolution	clim	soil	temp
Yearly soil temperature	Field measured	Site	-0.746	0.018	0.485
Yearly number of frost days	Remote sensing	Site	-0.854	0.247	0.317
Growing season length	Remote sensing	Site	-0.948	0.136	0.191
C/N	Field measured	Plot	0.289	-0.903	0.200
Organic matter content (%)	Field measured	Plot	-0.513	-0.816	0.067
Total nitrogen content ($\mu g.g^{-1}$ dw)	Field measured	Plot	-0.322	-0.842	-0.197
Nitrate content ($\mu g.g^{-1}$ dw)	Field measured	Plot	-0.568	0.472	-0.520
Ammonium content ($\mu g.g^{-1}$ dw)	Field measured	Plot	-0.735	0.075	-0.524
Microbial biomass N (gN g^{-1} dw)	Field measured	Plot	-0.629	0.231	0.017
Potential of N mineralization. (μgN.g dw.d^{-1})	Field measured	Plot	-0.658	-0.526	-0.226
Topographical water index	LiDar	Site	-0.657	0.102	0.316
Slope	LiDar	Site	0.391	0.291	0.297
Inertia			40%	24%	10%
Correlation with elevation			0.93	-0.16	-0.13

TABLEAU 2.1 – Environmental variable characteristics and scores along the first three axes of the PCA. The last two rows displays the part of inertia contained on each axis and its correlation with elevation

traits were only moderately correlated (with the strongest correlation between LDMC and foliar $\delta^{13}C$: r = 0.44, p < 0.001), we selected all functional traits and used euclidean distance to calculate pairwise functional distances between individuals. As there was missing trait data (3 out of 14140 trait values), we used the R-function *quasieuclid* (R-package ade4) to ensure that the functional distance matrix was euclidean. To calculate the functional distance between individuals while ignoring intraspecific variability, we replaced each individual trait value by the mean trait value of the species over the whole study area. We then used the procedure described above to calculate the pairwise functional distance matrix. The two functional distance matrices (with and without intraspecific variability) were then divided by the maximum distance value across both matrices to make the functional diversity metrics comparable.

We used the equivalent number of Rao's Quadratic Entropy [RAO, 1986] to calculate the diversity ${}^{\alpha}D_{ij}$ of community *j* belonging to site *i*, at a given grain size :

$$ {}^{\alpha}D_{ij} = [1 - \frac{1}{N^2}\sum_{k=1}^{N}\sum_{l=1}^{N} d_{kl}]^{-1} \tag{2.1} $$

N is the number of individuals in the community *j* belonging to site *i* (41) and $d_k l$ the Euclidean functional distance between individual *k* and *l* belonging to community *j* belonging to site *i*. To calculate the β-diversity within each site, at a given grain size, we

first calculated the γ-diversity ${}^{\gamma}D_i$ of the site i using Equation 2.1 applied to all individuals belonging to site i and to the studied grain size. The β-diversity of site i ${}^{\beta}D_i$ was then calculated as :

$$ {}^{\beta}D_i = {}^{\gamma}D_i \times \frac{1}{2}({}^{\alpha}D_{i1}^{-1} + {}^{\alpha}D_{i2}^{-1}) \tag{2.2} $$

Or in other terms, the β-diversity is calculated as the ratio of the site γ-diversity and the site mean α-diversity calculated as the harmonic mean of the diversity of the communities belonging to site i. Also because the distance matrix was euclidean, the diversity function is concave and the β-diversity is always superior or equal to 1 [PAVOINE, 2012]. Furthermore, this formulation allows to obtain estimates of within-site β-diversity that have a maximum value of 2 if communities of a given site contain fully dissimilar individuals [CHALMANDRIER et collab., 2015; LEINSTER et COBBOLD, 2012].

Null models

At a given spatial grain size, we used two null models to evaluate the deviation of functional and taxonomic α and β-diversities from a null hypothesis of random assembly from pools defined at two different spatial extents. First, we wanted to know if the α and within-site β-diversities deviate from what is expected if individuals are randomly distributed within communities regardless of their functional traits or their taxonomy. We called this model "the landscape null model". At a given grain size, random distributions were generated by randomly assigning without replacement 41 individuals from the 2020 sampled individuals to each of the 20 plots. Second, we wanted to know if the α and β-diversities deviate from what is expected if individuals are randomly distributed within the site regardless of their functional traits or their taxonomy [DE BELLO et collab., 2012]. We called this model "the site null model". At a given grain size, for each site, random distributions were generated by randomly assigning without replacement 41 individuals from the 101 sampled at this site to each of the two site plots. Each null model was run 10,000 times. For each α and β-diversities values we then calculated the standard effect size (SES) and rank of observed diversities in the two null models. The SES was calculated as the observed value minus the mean of the null distribution divided by the standard deviation of the null distribution. We accessed the significance of α or β-diversities using a two-sided test by calculating the proportion of random values that were below the observed value. If this rank value was below 0.05 (resp. higher than 0.95), the α or β-diversities were considered significantly low (resp. significantly high).

Multi-model inference

In total, we calculated for each of the twenty plots α-diversity (resp. each of the ten sites), the standard effect size (SES) of the α-diversity (resp. the within-site β-diversity) based on (1) functional distance without ITV or with ITV, (2) according to one of the four

spatial grains (3) and compared to one of the two spatial extents (landscape vs site null models). To analyze the drivers of community functional α-diversities, we developed a set of linear mixed models that included plots nested within sites as random effects and as possible fixed effects : (1) the three environmental gradients : climatic gradient (clim), soil parameters gradient (soil), local temperature gradient (temp) ; (2) ITV (as a categorical variable with modality "ITV", "noITV") ; (3) spatial grain (as a continuous variable with the smallest grain being attributed the value 0 and the largest the value of 3, thus proportional to the logarithm of community area) and (4) spatial extent (as a continuous variable with the site null model being attributed the value of 0 and the landscape null model being attributed the value of 1). We included two and three way interaction terms between one of the three environmental gradients, one of the two spatial scale components and ITV. The logic behind this interaction effect was to explicitly test whether the community response to environmental gradients was dependent on the two spatial scale components and on ITV.

From the full model containing all fixed effects and their interaction terms, we generated a set of all possible linear mixed models including a subset of these terms. Each model was fitted using a maximum likelihood approach. Models were then ranked according to the corrected Akaike information criterion (AICc) and their relative importance was evaluated with AICc weights [BURNHAM et ANDERSON, 2002]. We retained a confidence set of models with a cumulated AICc weight of 0.95 [JOHNSON et OMLAND, 2004]. The relative importance (RI) of each fixed effect in the confidence set was calculated as the sum of the Akaike weights over all of the models in which it appeared. We further calculated model averaged estimates of the fixed effects over the confidence set of models in which they were included and evaluated their significance [BURNHAM et ANDERSON, 2002].

As we included interactions in our model, the slope of functional α-diversities against an environmental gradient may return a significant interaction term with a cofactor because it is significantly different from the contrast modality but without the slope with said cofactor being significantly different from 0. We thus reran all the procedure for various sets of contrasts to ensure that our conclusions regarding the slope were appropriate. The same analysis was performed for within-site functional β-diversities, but with sites as a single random effect.

2.4 Complementary analyses

Single trait and taxonomic diversity indices

Multi-trait diversity metrics have been criticized for potentially mixing several independent axes of plant individual niches, ultimately blurring the signal of functional diversity responses to environmental gradients [SPASOJEVIC et SUDING, 2011]. To control for this, we studied community mean trait as well as functional diversity for each trait individually. Results are available in the supplementary material. We further studied taxono-

mic β-diversity. To do so, we use the same diversity indices but using an inter-individual distance matrix that contained 0 when pairs of individuals were conspecifics and 1 otherwise. We also confronted them to the null models described above.

Drivers of small-scale within-site functional heterogeneity

To understand the origin of the within-site heterogeneity, we tested the SES of functional β-diversities at the smallest spatial scale (grain of 1.25 by 1.25 m and small spatial extent) relative to two potential sources of heterogeneity. (1) Within-site functional heterogeneity could be first generated by a within-site taxonomic heterogeneity. If so, Z-statistics of functional β-diversities should be positively correlated to the Z-statistics of taxonomic β-diversities. This heterogeneity may arise because a patchy vegetation emerge due to short-range dispersion. (2) Conversely high within-site functional β-diversities may be caused by local topographical heterogeneity and/or local soil heterogeneity [CHOLER, 2005] filtering out different sets of individuals. If so, Z-statistics of functional β-diversities should be positively correlated to topographical and/or soil heterogeneity measures. Obtantion of these heterogeneity measures is explained in the supplementary material 8.1. If Z-statistics of functional β-diversities are also positively correlated with SES-statistics of taxonomic β-diversities, we expect that this would indicate habitat filtering of both species composition and functional traits t will further showed that this habitat filtering translate into different species composition between plots and not only in within-species trait response to different environments.

All analyses were conducted using R version 3.0.2 (R Core Development Team 2012) using the nlme [PINHEIRO et collab., 2007], MuMIn [BARTON, 2012] and snowfall [KNAUS et collab., 2009] packages.

3 Results

3.1 Patterns of α-diversity as a function of spatial grain and extent

Functional community α-diversities differed strongly as a function of both spatial extent and grain (Figure 2.2). When compared to null model draws, functional α-diversities appeared more convergent at larger spatial extent than at smaller extent (z-value : 15.88, RI = 1.00). In other terms, compared to the landscape-scale individual pool, communities were composed of functionally more similar individuals than randomly expected, while compared to the site pools, communities appeared to be randomly assembled with respect to their functional composition (Figure 2.3). Similarly, individuals co-occurred with functionally more similar individuals at a small grain than at a large grain (Figure 2.2, 2.3, 2.4). In other terms, when communities are defined on a small area, they tend to contain a more homogeneous vegetation in terms of functional traits compared to communities defined on a large area.

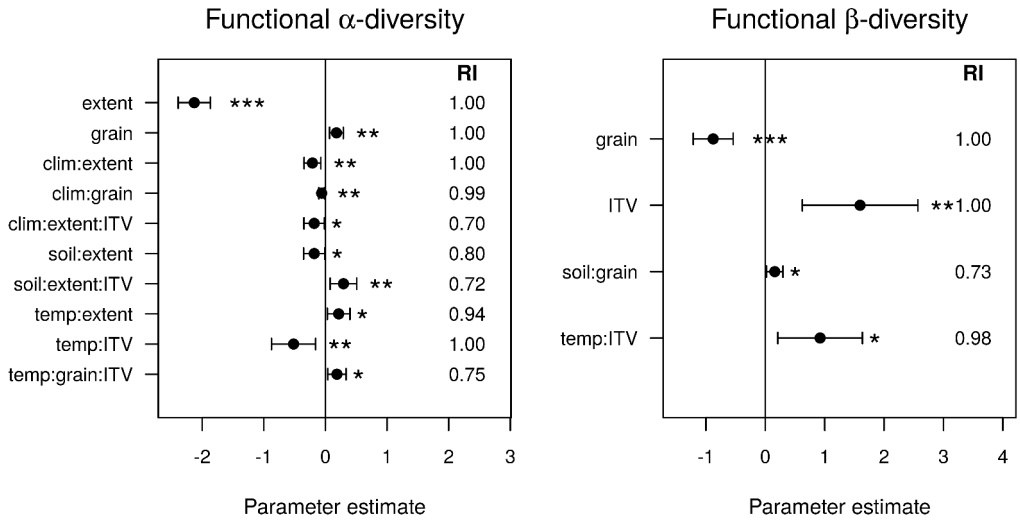

FIGURE 2.2 – Model averaged parameter estimates and 95% confidence intervals for fixed effects included in confidence set of models explaining the functional α and β-diversity of plots and sites. Relative importance (RI) is the sum of AIC weights of models in which a given predictor appears. Results are shown only for significant predictors with RI > 0.7. clim : climatic stress gradient ; soil : soil composition gradient ; temp : local temperature gradient ; ITV : inclusion of ITV.

3.2 Patterns of α-diversity across environmental gradients

Functional α-diversities of communities were linked to environmental gradients. Interestingly, this link was dependent on spatial scale and on ITV. Functional α-diversities had no relationship with the climatic stress gradient at a small spatial grain and extent but decreased significantly with climatic stress at a large spatial grain and extent (*clim :extent* z-value : 3.03, RI= 1.00 ; *clim :grain* z-value : 2.64, RI= 0.99). Accounting for ITV slightly reinforced this relationship (*clim :extent :ITV* z-value : 2.13, RI= 0.70). Single trait analyses revealed that Height, SLA and LCC α-diversities followed a similar pattern (although in the case of LCC only if ITV was included). In contrast, LDMC and foliar δ^{15}N α-diversities both increased with climatic stress (although only marginally for the latter, Table 2.2).

There was no significant relationship between community α-diversity and soil composition gradient. However community α-diversity was negatively linked to the local temperature gradient at small spatial grain and small spatial extent, but only when ITV was included (*temp :ITV* z-value : 2.84, RI = 1.00). However this pattern disappeared when the spatial grain or extent increased (*temp :grain :ITV* z-value : 2.45, RI = 0.75 temp :extent z-value : 2.39, RI = 0.94 ; Figure 2.2). Single trait studies revealed that LDMC was driving this pattern (Table 2.2).

3.3 Patterns of within-site β-diversity

Functional β-diversity was inversely linked to spatial grain with much higher functional turnover between communities at a small spatial grain. β-diversity was also significantly higher when ITV was included (*grain* estimate : -0.92, $p < 0.001$, RI = 1.00 ; *ITV*

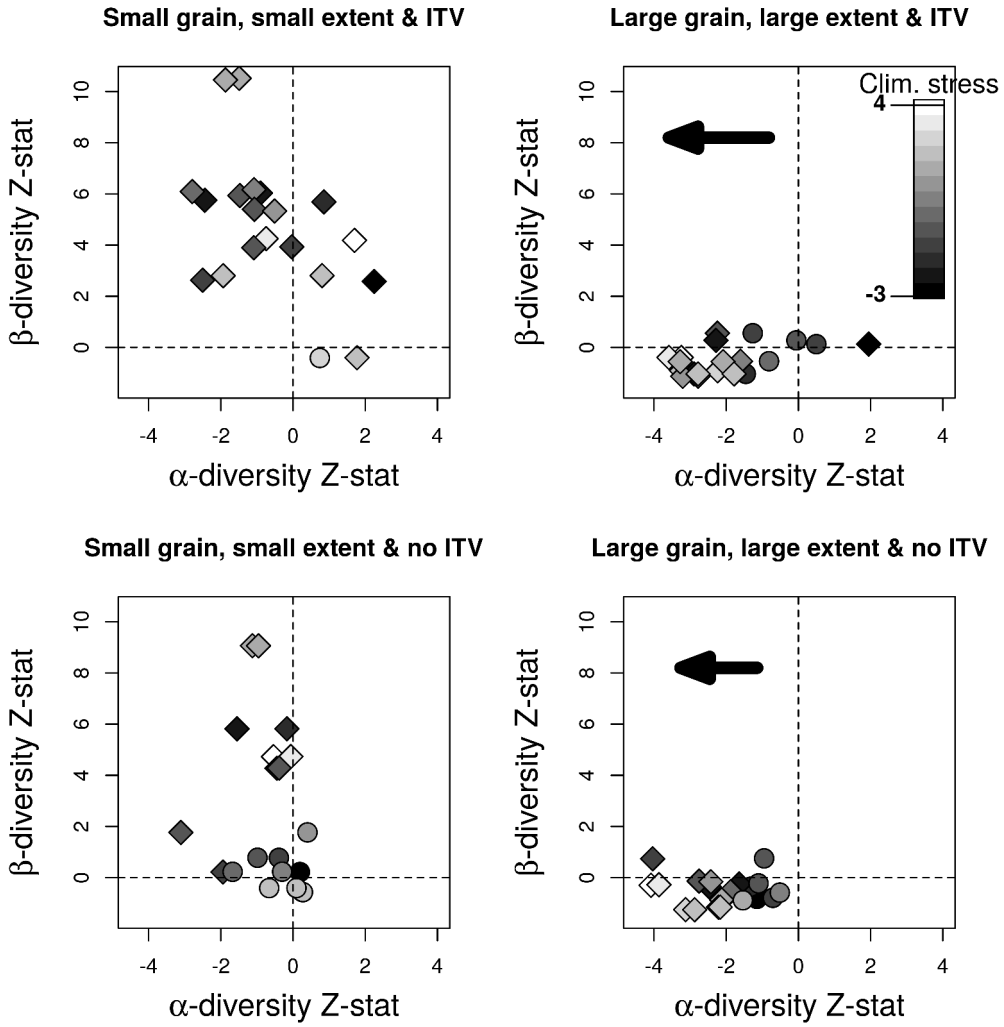

FIGURE 2.3 – Standardized effect size (SES) of community functional α-diversity plotted against the β-diversity SES of the site they belong to as a function of scale components, inclusion of intraspecific trait variability (ITV) and the climatic stress gradient. The color gradient symbolizes the level of climatic stress experienced by communities (black : warm end of the gradient, white : cold end of the gradient). Diamonds represent communities with significant α-diversity or within-site β-diversity (rank lower than 0.05 or higher than 0.95) ; circles represent communities with no significant α-diversity or within-site β-diversity. The arrows indicated the influence of the climatic stress (gradient on α and β SES. Their norm and direction against the x and y-axis are proportional to the averaged coefficient estimates given by the model averaging procedure. (If they were non significant or with limited relative importance (RI < 0.85), their norm was set to 0).

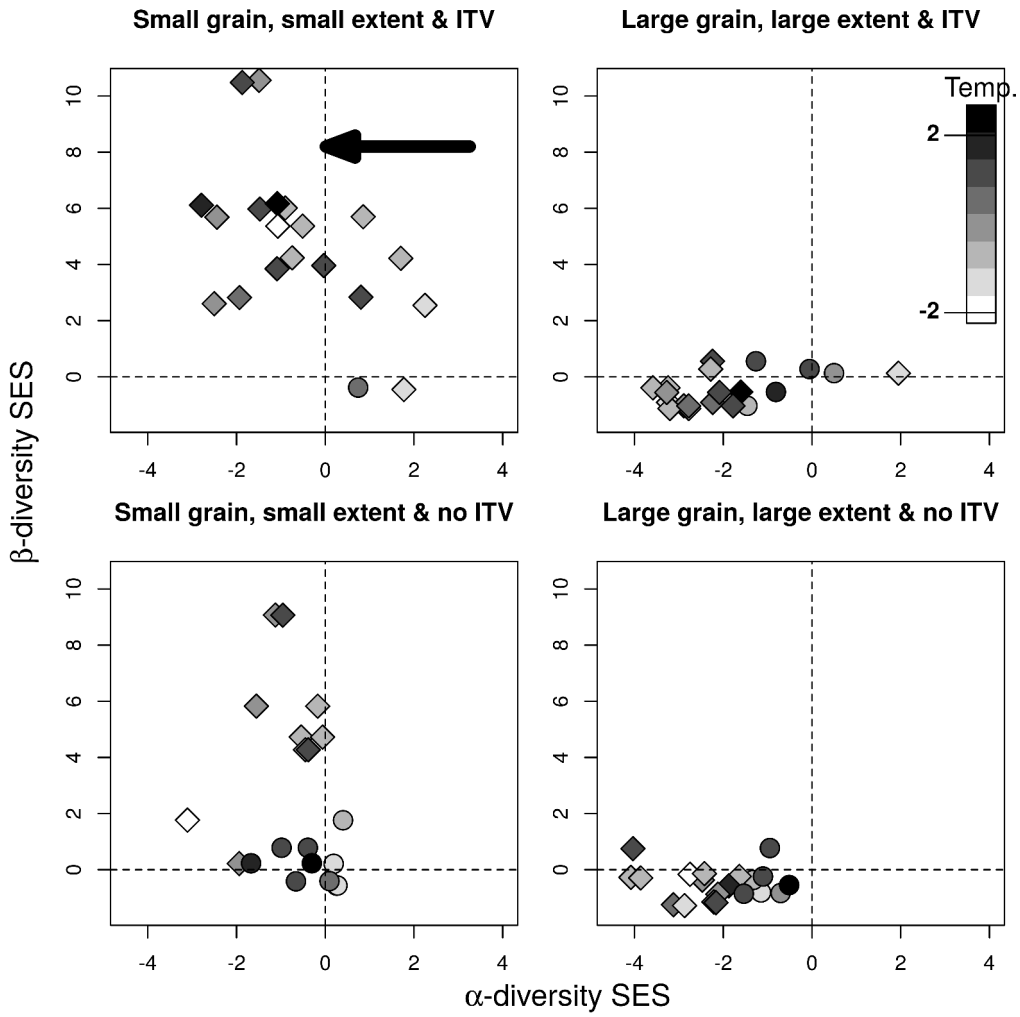

FIGURE 2.4 – Standardized effect size (SES) of community functional α-diversity plotted against the β-diversity SES of the site they belong to as a function of scale components, inclusion of intraspecific trait variability (ITV) and the local temperature gradient. The color gradient symbolizes the local temperature gradient experienced by communities (black : warm end of the gradient, white : cold end of the gradient). Diamonds represent communities with significant α-diversity or within-site β-diversity (rank lower than 0.05 or higher than 0.95) ; circles represent communities with no significant α-diversity or within-site β-diversity. The arrows indicated the influence of the climatic stress (gradient on α and β SES. Their norm and direction against the x and y-axis are proportional to the averaged coefficient estimates given by the model averaging procedure. (If they were non significant or with limited relative importance (RI < 0.85), their norm was set to 0).

Main conclusions	Trait driving	Trait countering
"Functional α-diversity decreased with increasing spatial extent and decreasing grain."	Height, SLA*, LDMC, LNC*, δ^{13}C*, δ^{15}N*	/
"Functional α-diversity decreased along the climatic stress gradient at large spatial extent and grain."	Height, SLA, LCC**	LDMC, (δ^{15}N)
"Functional α-diversity decreased along the local temperature gradient at small spatial extent and grain."	LDMC**	/
"Within-site β-diversity decreased with increasing spatial grain"	Height, SLA, LDMC, LCC, LNC, δ^{13}C, (δ^{15}N)	/
"Within-site β-diversity increased with the inclusion of ITV".	LCC, δ^{13}C	/

TABLEAU 2.2 – Summary of the congruence of functional diversity patterns with the pattern of traits studied individually. We classified traits as "driving traits" if they had a significant pattern (p-value lower than 0.05) going into the same direction of the overall functional syndrome and "countering traits" if they had a significant pattern going into the opposite direction. More complete results about the uni-trait models are available in the supplementary materials 2.7, 2.6. *No relationship to grain. ** Only significant if ITV is included. *** Only significant if ITV is not included.

estimate : 1.60, p = 0.0014, RI = 1.00). Functional β-diversity was neither significantly influenced by the climatic stress gradient nor by the soil and local temperature gradients. However, functional β-diversities had significantly different relations with the soil gradient according to the spatial grain (*soil :grain* estimate : 0.16, p = 0.024, RI = 0.73) and the local temperature gradient according to the inclusion of ITV (*temp :ITV* estimate : -0.63, p = 0.022, RI = 0.83), slope coefficients were not significantly different from 0 when changing the contrasts of the models.

Despite this lack of relationship to environmental gradients, single trait β-diversities revealed contrasting responses to environmental gradients (Supplementary material, Figure 2.8). At small spatial grain and extent and including ITV, within-site β-diversities of foliar δ^{13}C decreased while within-site β-diversities of foliar δ^{15}N increased along the climatic stress gradient. Furthermore, within-site β-diversities of LCC and foliar δ^{15}N decreased along the local temperature gradient while within-site β-diversities of foliar δ^{13}C decreased at a small grain when ITV was included.

3.4 Drivers of functional β-diversity at small spatial grain and extent

Taxonomic and functional β-diversities were positively related (Figure 2.5 ; Spearman's rank correlation : ρ = 0.20, p-value = 0.039 with ITV ; ρ = 0.88, p-value = 0.001, without ITV). Functional β-diversities were, however, not related to topographical heterogeneity (Figure 2.5 ; Spearman's rank correlation : ρ = 0.04, p-value = 0.91 with ITV ; ρ = -0.21, p-value = 0.56, without ITV) and were negatively related to soil heterogeneity (Figure 2.5 ;

Spearman's rank correlation : ρ = -0.39, p-value = 0.26 with ITV ; ρ = -0.67, p-value = 0.039, without ITV). This pattern was supported by the study of single trait β-diversities : spatial variation in individual plant height, SLA, LDMC, LCC and foliar δ^{15}N were positively linked to taxonomic β-diversities when ITV was ignored. No traits were positively linked to either measures of within-site habitat heterogeneity (Supplementary material - Table 2.3).

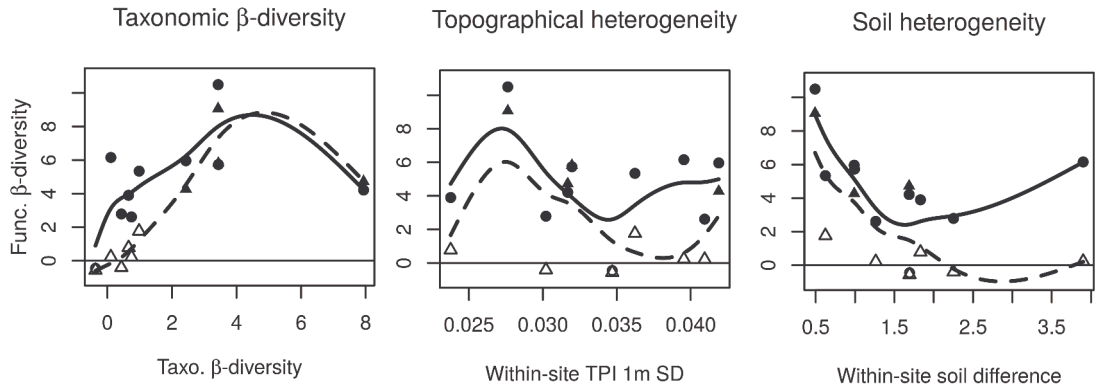

FIGURE 2.5 – Relationships between functional β-diversity at a small grain and a small spatial extent with three potential drivers. (1) The taxonomic β-diversity at a small grain and a small spatial extent, (2) within site topographic heterogeneity or (3) soil heterogeneity. Circles are β-diversity estimated with ITV ; triangles are β-diversity estimated without ITV. Sites with a β-diversity significantly high (rank higher than 0.95) are filled symbols. The regression lines (full line : with ITV ; dotted line : without ITV) was obtained from a generalized additive model.

4 Discussion

4.1 Overwhelming effects of spatial scale on diversity patterns

Our study stresses the importance of considering spatial grain and extent when studying functional diversity patterns of grassland communities. Considering these scale components, we were able to identify three main drivers of plant functional α-diversity in an Alpine valley : climatic filtering of traits at large spatial scales, filtering due to local temperature gradients and small-scale patchiness at a fine grain.

Our results validated our first hypothesis about a large-scale filtering due to climatic stress along an elevation gradient. At large spatial scale (large spatial extent and coarse grain), communities appeared the most functionally convergent (14 communities out of 20), as co-occurring individuals were more functionally similar than expected. This pattern is consistent with our first hypothesis of strong environmental filtering of functional traits at the landscape-scale [DE BELLO et collab., 2013]. In concordance with previous studies [DE BELLO et collab., 2013; HULSHOF et collab., 2013], communities tended to be functionally random or divergent at low stress levels (i.e. at the warmer end of the climatic gradient) and functionally convergent at high stress levels (i.e. colder end of the climatic gradient). The reason for this is that stressful conditions at high elevations require

that plant individuals possess certain functional traits or combinations of traits to persist (e.g. they need to be smaller, have a lower SLA...) thus constraining the local variability of functional traits. Conversely, LDMC α-diversity increased as well as foliar δ^{15}N (albeit marginally), and this may be explained by the fact that the diversity of both traits is associated with increasing diversity in resource use strategies : LDMC captures the trade-off between exploitative and conservative plant ecological strategies [DÍAZ et CABIDO, 1997] while foliar δ^{15}N captures more specifically plant nitrogen acquisition strategy [GUBSCH et collab., 2011]. We thus concluded that this pattern was due to a decrease in nitrogen availability with elevation (Table 2.1), which may promote niche partitioning in nitrogen use by local plant communities [ASHTON et collab., 2010; MICHELSEN et collab., 1996].

At a small spatial grain and extent, functional α-diversity was mostly random, as suggested by a previous study [CHALMANDRIER et collab., 2013]. Nonetheless, functional α-diversity still varied along the local temperature gradient. Small scale functional α-diversity was not linked to the climatic stress (nor the soil composition gradient). This refutes our second hypothesis that climatic stress impacts on functional α-diversity at small spatial grain and/or extent due to a shift from competition to facilitation as the main small-scale assembly processes [CALLAWAY et collab., 2002]. The same absence of pattern appeared when studying each trait diversity individually (Supplementary material, Figure 2.7).

However, we found out that community functional α-diversity increased along the local temperature gradient at a small spatial grain and extent when taking into account ITV. Interestingly this pattern was mainly driven by leaf dry matter content (Figure 2.7). Overall, it means that when taking into account the local pool of possible trait values, individuals tended to be spatially segregated at a fine grain and showed increased functional divergence in abnormally cold sites. We consider this to be a consequence of facilitation, with the local co-occurrence of more stress resistant individuals (with higher LDMC) and more stress sensitive individuals (with low LDMC) [CHOLER et collab., 2001; GROSS et collab., 2013].

Within-site functional β-diversity was much higher at small than at large spatial scale and was further supported by all single-trait β-diversity analyses (Table 2.2, Figure 2.8). We associated this pattern to the patchiness of alpine communities. When defined at a coarse grain (10x10m), communities were representative of the functional composition of the site and were thus similar within site. However when communities were sampled on a restricted area and compared to the local pool, we detected a certain degree of community functional patchiness. Functional β-diversity did not vary along environmental gradients, however this pattern actually hid contrasting responses of within-site β-diversity to environmental gradients between functional traits that compensated each other when calculating multi-trait functional β-diversity (Figure 2.8).

Functional β-diversity was only linked to taxonomic β-diversity and not to any measure of within-site habitat heterogeneity. While we may have misevaluated it, we conclude that local heterogeneity did not generate the functional patchiness of vegetation. We in-

terpreted it as a consequence of local reproduction, possibly favored by the clonality often exhibited by alpine plants [WITTE et collab., 2012] that likely generated the functional heterogeneity of the vegetation [POTTIER et collab., 2007].

4.2 Accounting for ITV reveals assembly rules at small spatial grain and extent

Our results show that it is only important to include ITV in certain settings. In contrasting to a previous study [SIEFERT, 2012], we found that the use of ITV did not significantly changed the value of α-diversity at large spatial extent and was not necessary to detect he relationship to large scale environmental gradients. Because of the important species turnover across the landscape, interspecific functional variability is likely to be the primary driver of meta-community diversity patterns.

More strikingly, at small spatial extent and fine grain, the inclusion of ITV was essential to detect the positive relationship between functional α-diversity and the local temperature gradient. More precisely, this was due to the underestimation of the functional divergence in communities at the stressful end of the gradient when ITV was ignored (Fibure 2.3). Therefore, it suggested that within-species trait variability (through ecotypic variation or trait plasticity) is in this case an important driver of niche differentiation and facilitative mechanisms at the cold end of the gradient. A possible mechanism is that facilitators belonged to functionally variable species that diverged from their species' mean trait syndrome to cope with the local conditions, while facilitated individuals belonged to less variable species and persisted by co-occurring with the more variable facilitators.

These findings confirm the hypothesis of [ALBERT et collab., 2011] about the scale-dependency of ITV, as well as the results of [SIEFERT et collab., 2014] about the importance of ITV in regards to local scale gradients. At a small scale, species turnover is less important and individuals are more functionally similar due to landscape scale filtering, and the local structure of communities is much more driven by the deviance of individuals from their species-level mean trait syndrome. This may reflect local adaptation or plasticity to cope with the very local environment.

5 Conclusion

Our study demonstrates how several ecological filters affect the assembly of alpine plant communities. Subalpine and alpine environments are highly constrained by steep landscape-scale gradients that have an overwhelming impact on diversity patterns. However this actually hides the influence of local gradients and biotic interactions on the structuring of subalpine and alpine community assembly. While experimental works have already demonstrated their importance, our study is showing how their print may actually emerge within landscape scale community diversity patterns. We highlight how varying

both grain size and extent can be decisive tools to uncover the effects of multiple ecological processes operating at different spatial scales. While varying spatial grain may require time-consuming field methods, varying spatial extent can be achieved simply through the use of constrained null models and furthermore provides a more complete picture of the assembly rules.

We confirmed the importance of intraspecific variability at the community scale and show that it is dependent on the two components of spatial scale : it is negligible at large spatial extent and grain but indispensable when studying local ecological processes, which confirms findings from previous studies. As measuring intra-specific variability is a time-consuming process, we recommend reserving its use to the study of local ecological processes. Finally, our results highlight the importance of within-species trait variability for understanding the mechanisms of species tolerance to local environmental gradients as well as the signature of facilitation on patterns of functional diversity. Future work should examine the mechanistic nature of this interplay between facilitation and intra-specific trait variability.

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8 Supplementary materials

8.1 Estimation of within-site topographic and soil heterogeneity

We evaluated two sources of within-site habitat heterogeneity. First, we computed within-site topographical heterogeneity by measuring in each site, the Topographic Position Index (TPI) at 1 by 1 m resolution. TPI measures the difference between a pixel altitude value and the mean elevation of the neighborhood around that cell. Positive value mean the cell is higher than its neighbors, while negative values mean it is lower. We then computed the standard-deviation of TPI for all 1x1m cells to obtain a single measure per site of topographical heterogeneity.

Second, we computed within-site soil heterogeneity. Soil sampling was similar to the one described in the main text expect that data came from three soil cores sampled in the smallest grain size community (1.25 by 1.25m).

From this dataset, we ran a Principal Component Analysis on the scaled soil variables to obtain uncorrelated axes. Then we compute the euclidean distance between plots of the same site as a measure of within-site soil heterogeneity.

8.2 Relationship between community mean trait and environmental gradients

Community mean trait was calculated as the mean trait of individuals per plot at a given grain size. They were then related to each of the three gradients (climatic stress, soil composition and local temperature anomaly), grain and the inclusion of ITV. As there was no null model associated with the community mean, there was no *extent*. Multimodel inference was run in a similar fashion than the main analysis.

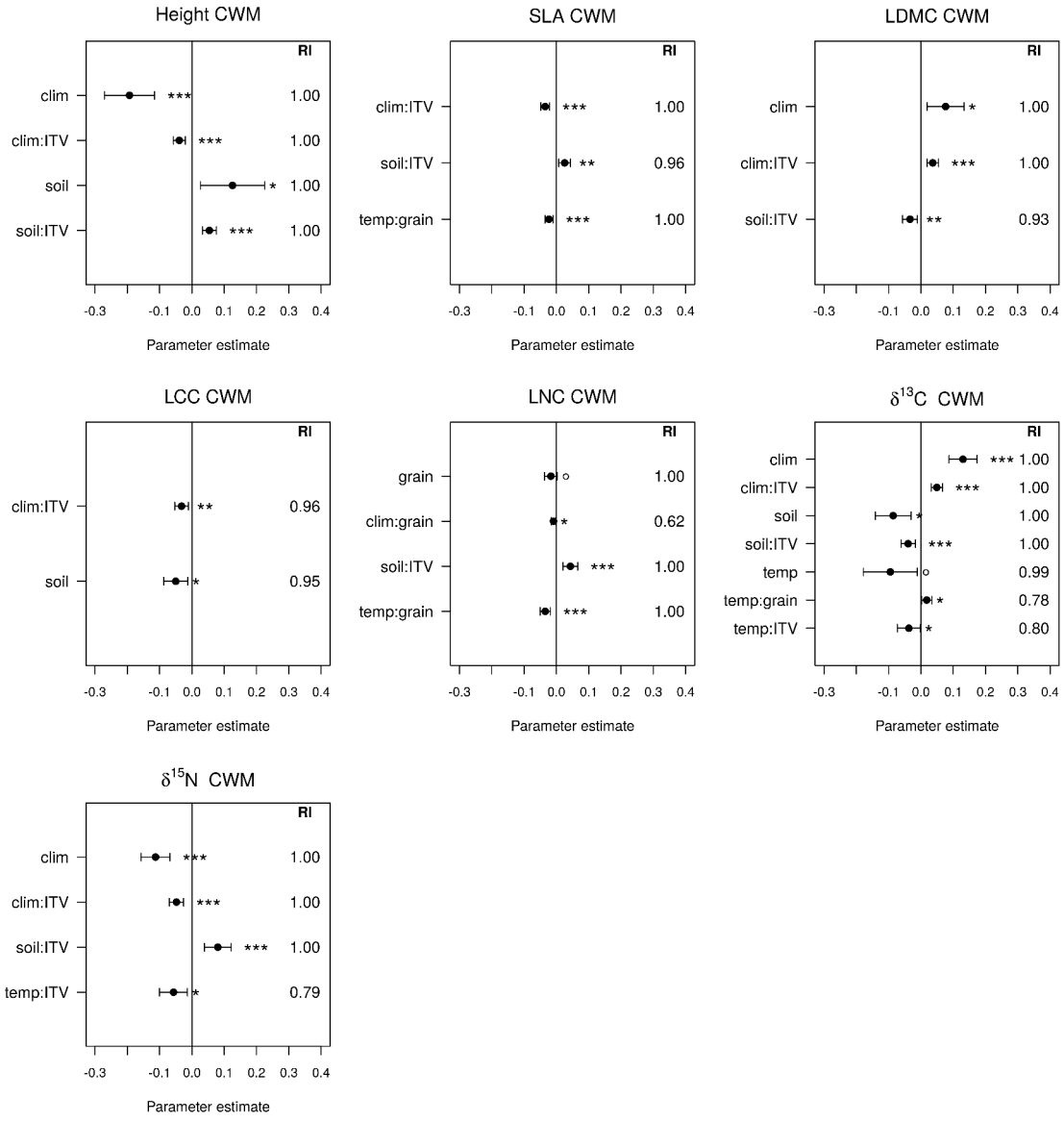

FIGURE 2.6 – Model averaged parameter estimates and 95% confidence intervals for fixed effects included in confidence set of models explainining community mean trait. Relative importance (RI) is the sum of AIC weights of models in which a given predictor appears. Results are shown only for predictors with RI > 0.60. clim : climatic stress gradient ; soil : soil structure gradient ; temp : local temperture gradient ; ITV : inclusion of ITV.

8.3 Relationship between community single trait diversity and environmental gradients

The same analysis as for multi-trait functional diversity was performed for each trait individually.

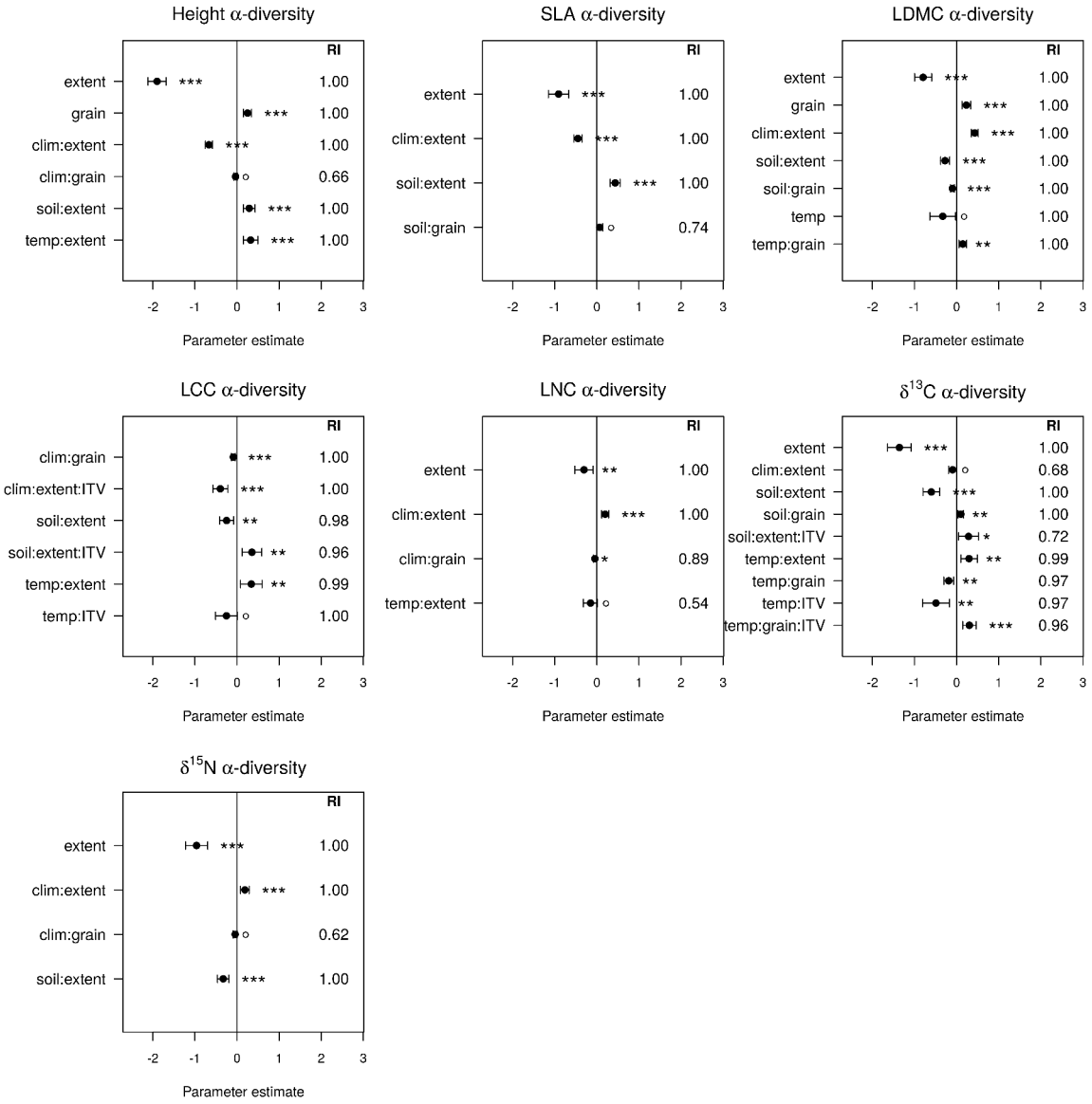

FIGURE 2.7 – Model averaged parameter estimates and 95% confidence intervals for fixed effects included in confidence set of models explainining community single trait α-diversities. Relative importance (RI) is the sum of AIC weights of models in which a given predictor appears. Results are shown only for predictors with RI > 0.60. clim : climatic stress gradient ; soil : soil structure gradient ; temp : local temperture gradient ; ITV : inclusion of ITV.

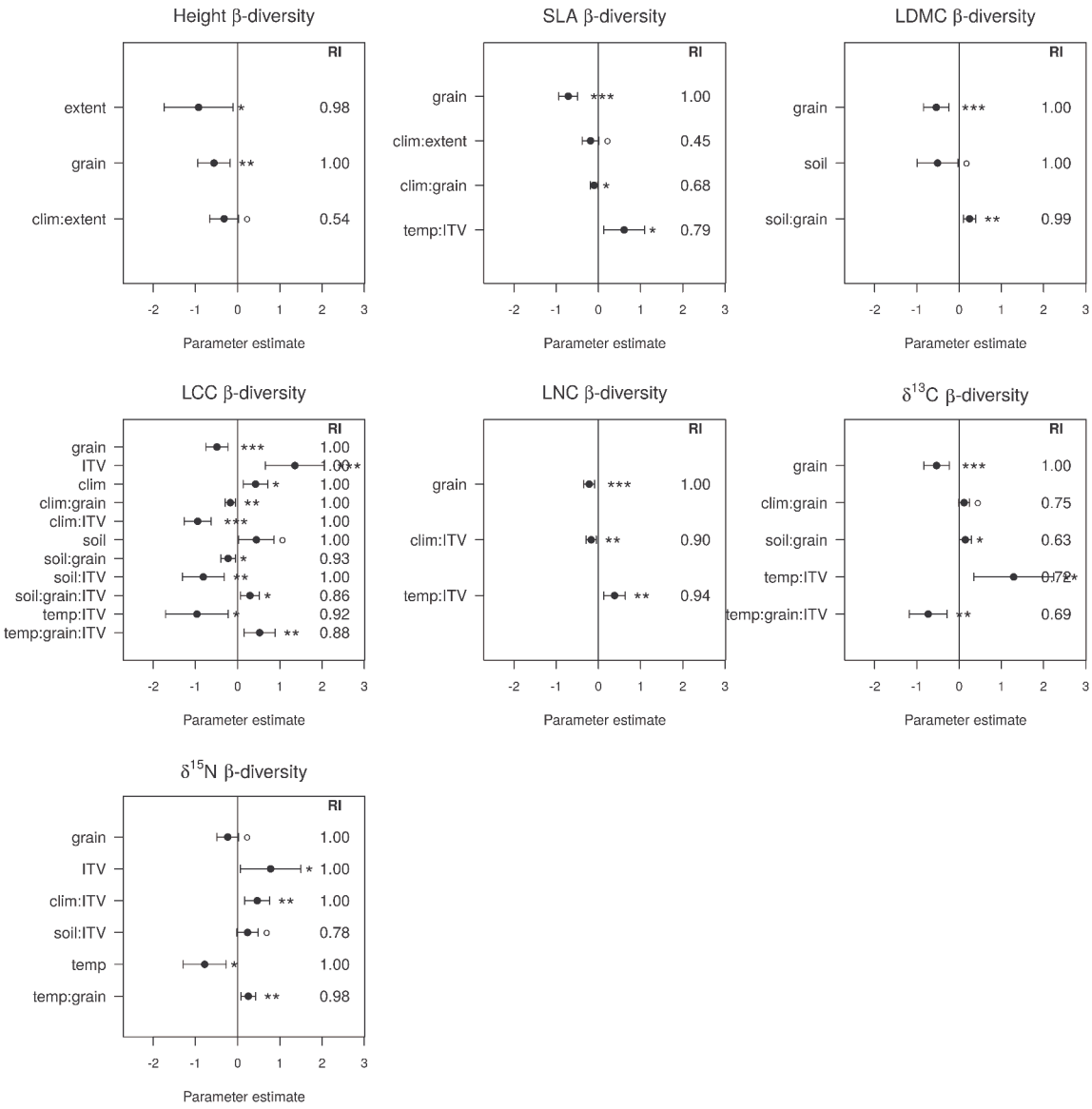

FIGURE 2.8 – Model averaged parameter estimates and 95% confidence intervals for fixed effects included in confidence set of models explainining site single trait β-diversities. Relative importance (RI) is the sum of AIC weights of models in which a given predictor appears. Results are shown only for predictors with RI > 0.60. clim : climatic stress gradient ; soil : soil structure gradient ; temp : local temperature gradient ; ITV : inclusion of ITV.

8.4 Relationship between community single trait β-diversity and local sources of heterogeneity

	Taxonomic β-diversity Z-stat		Within-site topographical heterogeneity		Within-site soil heterogeneity	
Trait	ITV	no ITV	ITV	no ITV	ITV	no ITV
Height	0.55 (0.10)	**0.81** (0.01)	0.05 (0.89)	0.26 (0.47)	-0.45 (0.19)	-0.44 (0.2)
SLA	0.26 (0.47)	**0.76** (0.02)	**-0.75** (0.02)	-0.10 (0.79)	-0.42 (0.23)	**-0.92** (0.01)
LDMC	0.38 (0.28)	**0.89** (0.01)	-0.09 (0.81)	-0.26 (0.47)	-0.26 (0.47)	-0.62 (0.06)
LCC	0.44 (0.20)	0.13 (0.73)	0.42 (0.23)	0.42 (0.23)	-0.59 (0.08)	0.02 (0.97)
LNC	0.02 (0.97)	**0.64** (0.05)	0.56 (0.10)	0.02 (0.97)	-0.10 (0.79)	**-0.71** (0.03)
$\delta^{13}C$	0.19 (0.61)	0.61 (0.07)	-0.27 (0.45)	-0.50 (0.14)	-0.07 (0.86)	-0.42 (0.23)
$\delta^{15}N$	0.5 (0.14)	**0.92** (0.01)	-0.59 (0.08)	0.05 (0.89)	-0.21 (0.56)	**-0.71** (0.03)

TABLEAU 2.3 – Spearman correlation coefficient and associated test p-value in brackets of single trait within-site β-diversity Z-stats at fine grain and small extent against : taxonomic β-diversity Z-stats at small grain and extent, within-site topographical heterogeneity or within-site soil heterogeneity. Significant ($p < 0.05$) correlation coefficients are in bold.

Deuxième partie

Décomposition α, β, γ des nombres de Hill - extensions méthodologiques

Introduction

Le concept de “diversité” d’une communauté est une notion pouvant faire référence à trois aspects de cette communauté : le nombre d’espèces (“plus les espèces sont nombreuses, plus la communauté est diverse”), le patron de dominance (“une communauté est moins diverse si une espèce est très dominante”) et la similarité de ses espèces (“plus les espèces sont différentes, plus la communauté est diverse”). De ces notions découle un grand nombre d’indices de diversité taxonomique, fonctionnelle et phylogénétique les prenant en compte différemment. De là découlent “la jungle des indices de diversité” [Ricotta, 2005] et les inventaires pour la défricher [Mouchet et collab., 2010; Pavoine et Bonsall, 2011; Tuomisto, 2010a,b].

On peut dire raisonnablement qu’aucun d’indice de diversité ne répond à toutes les attentes [Hurlbert, 1971] ; néanmoins parmi les différents indices, on peut distinguer la famille des nombres de Hill [1973] et ses extensions en indices de diversité fonctionnelles et phylogénétiques. Elle généralise en effet un grand nombre d’indices classiquement utilisés en écologie (ce qui montre un intérêt pratique certain) et par le fait qu’elle offre un cadre cohérent pour faire varier les hypothèses sur la prise en compte des abondances relatives des espèces et les similarités écologiques entre espèces.

Le but de cette introduction est d’exposer le cadre mathématique de ces indices de diversité, leurs propriétés ainsi que les perspectives qu’ils apportent pour l’étude des communautés et qui sont exploitées dans ce chapitre.

1 Prendre en compte l’abondance des espèces : les nombres de Hill

Les nombres de Hill sont des fonctions des abondances relatives des espèces dans une communauté. Ils quantifient la diversité d’une communauté avec le nombre d’espèce qu’elle contient, mais également par leur patron d’abondance. Ainsi ils prennent en compte l’idée qu’une communauté composée d’une espèce très dominante et deux espèces rares sera moins diverse qu’une communauté contenant ces trois espèces avec des abondances relatives égales.

1.1 Entropies et nombres équivalents

Les nombres de Hill dérivent d'une série de métriques appelées "entropies" utilisées en physique et en théorie de l'information. Dans le contexte d'une communauté composée d'espèces en différentes proportions, on peut définir l'entropie de la communauté comme l'incertitude dans l'identité d'un individu échantillonné dans cette communauté [JOST, 2006].

Ainsi si la communauté ne contient qu'une seule espèce, l'entropie de cette communauté sera nulle, car il n'y aura aucun doute sur l'identité d'un individu qui y serait échantillonné. Un autre exemple intuitif est fourni par l'entropie de TSALLIS [1988] ; pour une certaine paramétrisation, cette métrique donne l'indice de Gini-Simpson et s'exprime sous la forme : $H = 1 - \sum_i p_i^2$; avec p_i l'abondance relative de l'espèce *i*. Cette formule est égale à la probabilité d'échantillonner dans la communauté deux individus appartenant à deux espèces différentes.

De ces indices d'entropie, une transformation monotonique permet d'obtenir un indice de diversité de la communauté *stricto sensu*, c'est-à-dire le nombre d'éléments effectifs dans l'objet observé. Dans le contexte de l'étude d'une communauté, ce nombre effectif est défini comme le nombre d'espèces d'une communauté de diversité équivalente où toutes les espèces auraient la même abondance [JOST, 2006]. Pour cette raison, cet indice a été nommé "nombre équivalent" [MACARTHUR, 1965], "nombre effectif", "nombre de Hill", voire même "indice de diversité vraie" [TUOMISTO, 2010a].

1.2 Formulation des nombres de Hill

HILL [1973] formalisa une unique formule qui permet de regrouper ensemble les indices très utilisés que sont la richesse spécifique et l'entropie de Shannon ou l'indice de Gini-Simpson mis sous forme de nombres équivalents. La diversité d'une unité spatiale (ex. : communauté, région) contenant *N* espèces s'exprime alors sous la forme :

$$ {}^{q}\mathrm{D}(\mathrm{P}) = \begin{cases} [\sum_{i=1}^{\mathrm{N}} p_i^q]^{1/(1-q)} & q \neq 1 \\ exp[-\sum_{i=1}^{\mathrm{N}} p_i \times log(p_i)] & q = 1 \\ max_i(p_i)^{-1} & q \to \infty \end{cases} $$

Avec le vecteur $\mathrm{P} = \{p_1, p_2, ..., p_{\mathrm{N}}\}$ tel que $\sum_i p_i = 1$

Leurs équivalents entropiques sont les entropies de TSALLIS [1988] :

$$ {}^{q}\mathrm{H}(\mathrm{P}) = \begin{cases} \frac{1}{1-q} \times (\sum_{i=1}^{\mathrm{N}} p_i^q - 1) & q \neq 1 \\ -\sum_{i=1}^{\mathrm{N}} p_i \times log(p_i) & q = 1 \end{cases} $$

Le passage d'une mesure d'entropie à son équivalent en nombre effectif se fait par la fonction d'exponentielle déformée TSALLIS [1994] et la transformation inverse par sa

fonction réciproque : le logarithme déformé.

$$ln_q(x) = \begin{cases} \frac{1}{1-q} \times (x^{1-q} - 1) & q \neq 1 \\ ln(x) & q = 1 \end{cases}$$

$$exp_q(x) = \begin{cases} (1 + (1-q)x)^{1/(1-q)} & q \neq 1 \\ exp(x) & q = 1 \end{cases}$$

Alors $ln_q({}^q\mathrm{D}(\mathrm{P})) = {}^q\mathrm{H}(\mathrm{P})$ et ${}^q\mathrm{D} = exp_q({}^q\mathrm{H})$

Le paramètre q contrôle le poids donné aux espèces dominantes par rapport aux espèces rares. Lorsque q est égal à 0, toutes les espèces contribuent également à la somme à l'origine de la valeur de diversité. Lorsque q augmente, plus de poids est accordé aux espèces dominantes par rapport aux espèces rares jusqu'à ce que la diversité de la communauté ne dépende plus que de l'abondance relative de l'espèce la plus dominante. On voit que ces familles d'indices unifient avec une unique formule paramétrique un grand nombre d'indices de diversité ou d'entropie classique : le nombre d'espèces (${}^0\mathrm{D}(\mathrm{P})$), l'entropie de Shannon (${}^1\mathrm{H}(\mathrm{P})$), l'indice de Gini-Simpson (${}^2\mathrm{H}(\mathrm{P})$), l'inverse de Simpson (${}^2\mathrm{D}(\mathrm{P})$) et d'autres moins connus [Hill, 1973; Jost, 2006; Leinster et Cobbold, 2012].

Cette famille d'indices a de nombreuses propriétés jugées désirables par les écologues Jost [2007]; Ricotta [2005]; Routledge [1979]. On peut citer :

— Quel que soit le vecteur des abondances relatives et le paramètre q, la valeur de ${}^q\mathrm{D}$ sera comprise entre 1 et N (le nombre d'espèces) ; 1 correspond au cas où une espèce est tellement dominante qu'elle constitue l'essentiel de la communauté, tandis que le maximum N est atteint quand toutes les espèces de la communauté ont la même abondance relative, autrement dit la communauté est « régulière », et ce quelque soit la valeur de q (Jost 2007).

— La diversité d'une communauté augmente si on remplace un individu de la communauté par un individu d'une espèce qui y était absente ou si on remplace un individu d'une espèce a de la communauté par un individu d'une espèce b dont l'abondance relative est plus faible que celle de l'espèce a (Ricotta 2005) : cette notion est appelée "concavité de Shur".

— Enfin, les entropies sont des fonctions concaves, ce qui implique que l'entropie d'un mélange de deux communautés est toujours supérieure ou égale à la moyenne arithmétique des entropies des deux communautés définie par les vecteurs d'abondances relatives d'espèces P_1 et P_2.

$${}^q\mathrm{H}(\omega_1\mathrm{P}_1 + (1-\omega_1)\mathrm{P}_2) \geq \omega_1 \times {}^q\mathrm{H}(\mathrm{P}_1) + (1-\omega_1) \times {}^q\mathrm{H}(\mathrm{P}_2) \quad \forall \omega_1 \in [0,1]$$

1.3 Décomposition en diversité α, β et γ

À partir de ces indices, il devient possible de décomposer la diversité d'une méta-communauté (c'est-à-dire un ensemble de communautés) selon la formulation proposée par WHITTAKER [1960] entre la diversité moyenne contenue dans les communautés (diversité $\bar{\alpha}$), la diversité régionale (diversité γ) et la diversité en communautés (diversité β). De nombreuses discussions ont eu lieu récemment pour déterminer la meilleure manière de calculer la diversité β, notamment sur le choix d'une décomposition additive : $\gamma = \beta + \bar{\alpha}$ ou multiplicative $\gamma = \beta \times \bar{\alpha}$ [JOST, 2007; TUOMISTO, 2010a]. Depuis un certain consensus a émergé pour restreindre la décomposition multiplicative aux nombres équivalents obtenus avec ${}^{q}D$ et la décomposition additive aux entropies ${}^{q}H$ [JOST, 2007; MARCON et collab., 2015].

Pour calculer les diversités $\bar{\alpha}$, β et γ d'ordre q d'une méta-communauté contenant S communautés, on définit les vecteurs d'abondances relatives de chaque communauté : P_1, P_2,... P_S et les pondérations de chaque communauté : ω_1, ω_2,... ω_S ($\forall i, \quad \omega_i \geq 0$ & $\sum_i \omega_i = 1$). Ces pondérations représentent l'importance attribuée à chaque communauté pour définir la méta-communauté. Alors on peut quantifier les diversités ${}^{q}\alpha$, ${}^{q}\beta$ et ${}^{q}\gamma$ ainsi [TUOMISTO, 2010a] :

$$ {}^{q}\gamma = {}^{q}D(\sum_i \omega_i P_i) $$

$$ {}^{q}\bar{\alpha} = [\sum_i \omega_i \times {}^{q}D(P_i)^{(1-q)}]^{1/(1-q)} $$

$$ {}^{q}\beta = \frac{{}^{q}\gamma}{{}^{q}\bar{\alpha}} $$

Un point important de cette formule est que la moyenne des diversités d'un ensemble de communautés doit être calculée avec une moyenne généralisée d'ordre *1-q*; ceci est en fait équivalent à faire la moyenne arithmétique des entropies des communautés et la convertir en nombre effectif avec la fonction d'exponentielle déformée. Le non-usage de cette moyenne généralisée (en général substituée par une simple moyenne arithmétique) a donné lieu à des mauvaises interprétations des propriétés mathématiques des nombres équivalents (ex. la "non-concavité" de ${}^{2}D(P)$, LANDE [1996]).

Cette décomposition multiplicative des nombres équivalents présente les propriétés suivantes [JOST, 2007] :

— La diversité β est indépendante des diversités γ et $\bar{\alpha}$ de la zone d'étude [BASELGA, 2010]. Cela présente l'avantage de rendre facilement comparables les diversités β de régions avec des diversités $\bar{\alpha}$ différentes (ex. DEVICTOR et collab. [2010]).

— La diversité β est comprise entre 1 (si les unités spatiales sont identiques) et le nombre de d'unités spatiales (si elles sont complètement distinctes). Le fait que la diversité β soit toujours supérieure ou égale à 1 est due à la concavité de la métrique

d'entropie dont elle est dérivée (voir plus haut). Ainsi, l'intervalle de valeurs de la diversité β est seulement dépendant du nombre d'unités échantillonnées et peut être facilement rééchelonnée entre 0 et 1 [CHAO et collab., 2012]. Cette transformation peut se révéler utile lorsqu'on compare des régions n'ayant pas subi le même effort d'échantillonnage (ex. FICETOLA et collab. [2013]).

1.4 Intérêt du paramètre *q* pour l'analyse de la diversité des communautés

Au-delà de la beauté formelle d'unifier un grand nombre d'indices de diversité populaires, ce cadre d'analyse permet d'étudier la diversité de communautés en faisant varier le paramètre q plutôt que via le choix arbitraire d'un unique indice de diversité. Cela génère "un profil de diversité" [LEINSTER et COBBOLD, 2012].

Ainsi le classement de plusieurs communautés peut changer selon la paramétrisation de l'indice de diversité, car la distribution de l'abondance relative des espèces d'une communauté est typiquement non uniforme [VOLKOV et collab., 2003], avec un petit nombre d'espèces représentant la majorité de la biomasse ou du nombre d'individus présents dans la communauté, et la plupart des autres espèces sont rares.

L'exemple illustré dans la Figure 2.9 illustre l'impact de cette paramétrisation. En effet, l'exemple montre que pour une valeur de q proche de ou égale à 0, le classement en diversité des communautés est (1)>(2)>(3), alors que pour une valeur de q élevée (supérieure à 1), le classement devient (3)>(2)>(1). On peut expliquer cela en supposant que la communauté 1 contient un grand nombre d'espèces rares et un petit nombre d'espèces très dominantes alors que la communauté (3) contient un plus petit nombre d'espèces, mais avec un patron de dominance moins marqué. Pour un nombre équivalent calculé avec une faible valeur de q, la communauté (1) apparaît donc plus diverse que la communauté (3) à cause du grand nombre d'espèces rares. En revanche pour une forte valeur de q, les espèces rares n'influent plus la quantification de la diversité et la communauté (3) paraîtra plus diverse à cause de son plus grand nombre d'espèces dominantes par rapport à la communauté (1).

Cela a deux implications. En premier lieu, le choix d'un indice de diversité pour estimer le patron de diversité n'est pas anodin et peut changer drastiquement le résultat de l'analyse. Faire varier le paramètre q revient à tester l'influence de choix méthodologiques sur les conclusions à tirer de l'étude.

En second lieu, une méthodologie basée sur les nombres de Hill peut être utilisée pour tester si certaines règles d'assemblage sont plus évidentes quand on concentre l'étude sur les espèces dominantes ou sur l'ensemble des espèces. BOULANGEAT et collab. [2012a] ont ainsi montré que la composition d'une communauté (c'est à dire le nombre d'espèces et leur identité) est contrainte par le filtre abiotique tandis que le patron d'abondances des espèces est le résultat des interactions biotiques et de la limitation de la dispersion. Dans

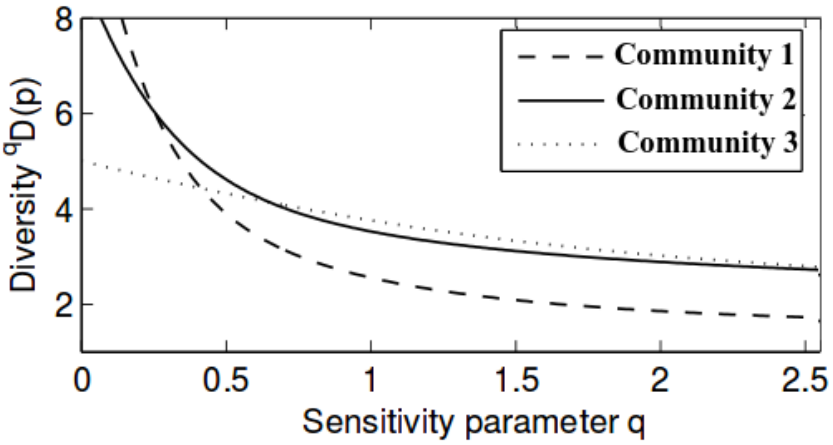

FIGURE 2.9 – Comparaison de la diversité de trois communautés en fonction du paramètre q (adapté de LEINSTER et COBBOLD [2012]).

le même ordre d'idée, LEVINE et collab. [2004] ont suggéré que la compétition est peu susceptible d'empêcher l'introduction de nouvelles espèces (invasives) dans une communauté, mais qu'en revanche elle est susceptible de maintenir son abondance à un niveau faible ; en reformulant dans le cadre des règles d'assemblage, les auteurs concluaient donc que l'exclusion compétitive ne pouvait modifier la composition d'une communauté, mais qu'en revanche elle influence fortement la structure de dominance de la communauté.

Dans ce cadre théorique, on peut faire l'hypothèse générale qu'une étude de patrons de diversité basée sur une valeur de q faible sera plus susceptible d'observer l'influence des filtres abiotiques de la zone d'étude tandis qu'une étude basée sur une valeur de q plus élevée est plus susceptible de mettre en évidence l'influence des interactions biotiques. Au final, cette famille d'indices de diversité peut être utilisée pour discerner la hiérarchie des filtres qui viennent déterminer la composition puis le patron d'abondance et enfin les espèces dominantes.

2 Inclusion des similarités interspécifiques

L'intérêt d'inclure la similarité entre espèces revient à reconnaître que certaines espèces sont moins distinctes que d'autres. Intuitivement, il est légitime de considérer qu'une communauté contenant trois espèces végétales du genre *Poa* est moins diverse qu'une communauté contenant une espèce végétale de *Poa*, une espèce de *Trifolium* et une espèce d'*Aster*, et ce malgré le fait que les deux communautés ont le même nombre d'espèces.

Par ailleurs, comme nous l'avons vu dans l'introduction, la métrique de similarité écologique est reliée à la notion de similarité de niche écologique et à la détection des règles d'assemblage. C'est pourquoi il a été proposé des extensions des nombres de Hill permettant d'inclure des mesures de similarité écologique entre espèces.

2.1 Adaptation aux nombres équivalents

De la même façon que l'estimation de la diversité taxonomique des communautés a été unifiée autour des nombres de Hill, de nombreux auteurs ont proposé des généralisations en dérivant pour unifier les indices de diversité fonctionnelle et phylogénétique, c'est-à-dire en considérant une similarité variable entre espèces [Chao et collab., 2010; Leinster et Cobbold, 2012; Pavoine et collab., 2009]. On peut distinguer deux écoles qui diffèrent par la façon d'intégrer les dissimilarités interspécifiques : la première [Chao et collab., 2010; Pavoine et collab., 2009] intègre la similarité entre espèces obtenues à partir d'arbres de dissimilarités fonctionnelle et phylogénétique. La deuxième [Leinster et Cobbold, 2012] se base sur une matrice de similarité entre espèces, en général estimée à partir d'une matrice de distances fonctionnelle ou phylogénétique entre espèces (en première approximation qui peut être calculée par la formule :

$$z_{ij} = 1 - \frac{d_{ij}}{max_{ij}(d_{ij})}$$

avec d_{ij} la distance fonctionnelle ou phylogénétique entre l'espèce i et j et z_{ij} la similarité utilisée par l'indice de Leinster).

Comme les nombres de Hill, les indices de Chao généralisent des indices de diversité fonctionnelle et phylogénétique connus (cf. Tableau 2.4), tel que l'indice de Faith [1992] ou de Petchey et Gaston [2007] (q égal à 0). Par ailleurs, leurs pendants entropiques comprennent l'entropie de Allen et collab. [2009] pour q égal à 1 et l'entropie quadratique de Rao [1986] appliquée aux arbres pour q égal à 2.

Comme la famille d'indices de Chao, les indices de Leinster & Cobbold regroupent également un certain nombre d'indices de diversité fonctionnelle ou phylogénétique : l'entropie quadratique de Rao ainsi que les entropies de Ricotta et Szeidl [2006]. Le fait que ces indices sont basés sur des matrices de similarité est un atout non négligeable pour les études de diversité fonctionnelle où la donnée de similarité n'est pas basée sur des arbres, mais des distances fonctionnelles. La transformation en arbre de la matrice de distance amène une perte importante de la variance [Petchey et Gaston, 2007], ce qui, est quelque peu "frustrant pour les écologistes de terrain connaissant les difficultés rencontrées pour mesurer tous ces traits" (in Marcon et collab. [2015]) .

2.2 Propriétés

Comme les nombres de Hill, ces indices de diversité sont compris entre 1 et N, le nombre total d'espèces dans la communauté. La valeur maximale N est atteinte si toutes les espèces sont également et complètement dissimilaires entre elles et en égales abondances [Chiu et collab., 2013; Leinster et Cobbold, 2012].

En revanche, contrairement aux nombres de Hill, il a été montré pour l'entropie quadratique de Rao qu'elles ne respectent pas la concavité de Shur car l'ajout d'une espèce

	Indice de Chao	Indice de Leinster
q = 0	${}^0\mathrm{D}(\mathrm{P_B},\mathrm{L_B}) = \sum_b \frac{\mathrm{L}_b}{\mathrm{T}}$	${}^q\mathrm{D}(\mathrm{P},\mathrm{Z}) = \sum_i p_i (\mathrm{ZP})_i^{-1}$
q = 1	${}^1\mathrm{D}(\mathrm{P_B},\mathrm{L_B}) = exp(-\sum_b \frac{\mathrm{L}_b}{\mathrm{T}} \times p_b \times log(p_b))$ *Exponentielle de l'entropie d'Allen*	${}^1\mathrm{D}(\mathrm{P},\mathrm{Z}) = exp(-\sum_i p_i \times log((\mathrm{ZP})_i))$ *Exponentielle de l'entropie de Ricotta & Szeidl*
q = 2	${}^2\mathrm{D}(\mathrm{P_B},\mathrm{L_B}) = (\sum_b \frac{\mathrm{L}_b}{\mathrm{T}} \times p_b^2)^{-1}$ *Transformation de l'entropie quadratique de Rao*	${}^q\mathrm{D}(\mathrm{P},\mathrm{Z}) = (\sum_i \sum_j z_{ij} p_i p_j)^{-1}$ *Transformation de l'entropie quadratique de Rao*
q	${}^q\mathrm{D}(\mathrm{P_B},\mathrm{L_B}) = (\sum_b \frac{\mathrm{L}_b}{\mathrm{T}} \times p_b^q)^{\frac{1}{1-q}}$	${}^q\mathrm{D}(\mathrm{P},\mathrm{Z}) = (\sum_i p_i (\mathrm{ZP})_i^{q-1})^{1/(1-q)}$

TABLEAU 2.4 – Bilan des indices de CHAO et collab. [2010] et LEINSTER et COBBOLD [2012]. $\mathrm{P_B} = \{p_b\}$ et $\mathrm{L_B} = \{\mathrm{L}_b\}$ sont respectivement le vecteur des abondances et le vecteur des longueurs des branches de l'arbre fonctionnel ou phylogénétique. L'abondance d'une branche est calculée en faisant la somme des abondances de ses descendants. T est la longueur de branche séparant la racine des feuilles de l'arbre phylogénétique ou fonctionnel. $\mathrm{P} = \{p_i\}$ est le vecteur des abondances relatives des N espèces présentes dans la communauté. $\mathrm{Z} = \{z_{ij}\}$ est la matrice des mesures de similarité des N espèces. NB : $(\mathrm{ZP})_i = \sum_j z_{ij} p_j$

peut diminuer la diversité de l'assemblage si cette espèce est trop similaire à celle déjà présente dans la communauté [RICOTTA, 2005]. Cela peut être corrigé par l'utilisation d'une matrice de distances ultra-métriques [PAVOINE et collab., 2005], bien que la désirabilité d'un indice respectant la concavité de Shur est affaire de perspective [PAVOINE, 2012]. L'ultramétricité se définit par les propriétés suivantes : une matrice $\mathrm{D} = (d_{kl})$ est ultramétrique si :

$$(i) \quad d_{kl} = d_{lk}; d_{kk} = 0 \quad \forall k, l$$

$$(ii) \quad \forall k, l, m \quad d_{kl} \leq max(d_{km}, d_{ml})$$

CHIU et collab. [2013] ont démontré que la décomposition multiplicative faite en utilisant la généralisation de Chao des nombres de Hill possède également les propriétés exposées dans la partie "Décomposition de la diversité", quelque soit l'arbre utilisé.

En revanche, ce n'est pas le cas de l'indice de Leinster, l'utilisation d'une matrice de similarité peut entraîner la perte de concavité (classique) de la fonction de diversité, ce qui implique que la diversité β peut alors être inférieure à 1. Ainsi pour l'entropie quadratique de Rao (qui correspond à q égal à 2, pour l'indice de Leinster & Cobbold), il a été montré qu'il fallait que la matrice de distances $\mathrm{D} = (d_{kl})$ respecte deux conditions [PAVOINE, 2012; RAO, 1986] :

$$(i) \quad d_{kl} = d_{lk}; d_{kk} = 0 \quad \forall k, l$$

$$(ii) \quad \forall a_1, a_2, \ldots \text{ si } \sum_k a_k = 0 \text{ alors } \sum_k \sum_l a_k a_l d_{kl} \leq 0$$

Néanmoins à ma connaissance, une telle propriété n'a pas été généralisée à toute valeur de q, ce qui rend difficile l'utilisation de l'indice de Leinster & Cobbold sans arrière pensée pour décomposer la diversité d'une méta-communauté en diversités $\overline{\alpha}$, β et γ. C'est pourquoi on se restreindra au cas des indices de Chao par la suite.

2.3 Estimer la similarité écologique à partir de la distance phylogénétique ou fonctionnelle

Variété des approches

La façon la plus intuitive et la plus employée pour calculer la similarité écologique entre espèces consiste à utiliser directement l'arbre fonctionnel ou phylogénétique dans le cas des indices de Chao. Concrètement sachant que l'arbre sert à estimer la similarité écologique, cela revient à supposer que la similarité écologique entre espèces varie linéairement avec les distances fonctionnelles et évolutives (ex. WEBB et collab. [2002], MASON et collab. [2005]).

Des études récentes ont montré que la similarité écologique entre espèces peut ne pas avoir une relation linéaire avec la distance phylogénétique [GODOY et collab., 2014]. De plus, il a été montré qu'il n'y a pas de fondement théorique solide pour affirmer cette relation linéaire, LETTEN et CORNWELL [2014] ont ainsi montré que dans l'hypothèse d'un scénario d'évolution brownienne des traits (cf. Introduction), la distance fonctionnelle entre espèces a plutôt tendance à être corrélée à la racine carrée de la distance phylogénétique et que cette transformation améliore la puissance des analyses de patrons de diversité [HARDY et PAVOINE, 2012; LETTEN et CORNWELL, 2014]. Concrètement, cela indique que les différentes parties de l'arbre phylogénétique sont moins pertinentes que d'autres pour estimer la distance écologique entre espèces et que leur donner un trop grand poids peut masquer le signal de règles d'assemblage.

Conceptuellement, cela rejoint les approches pionnières pour estimer la diversité fonctionnelle. Ainsi TILMAN et collab. [1997] ne quantifiaient pas la diversité à partir des distances fonctionnelles, mais en comptant les groupes fonctionnels d'une communauté, qui peuvent eux-mêmes être inférés à partir de données de traits fonctionnels BOULANGEAT et collab. [2012b]. Or la définition d'un groupe fonctionnel se fait typiquement en coupant un arbre fonctionnel à un certain seuil pour définir des groupes fonctionnels ; donc à supposer une relation en créneau pour estimer la similarité écologique entre espèces : si la similarité fonctionnelle entre deux espèces est supérieure à ce seuil, elles sont considérées comme fonctionnellement indiscernables et dans l'autre cas, comme fonctionnellement complètement dissimilaires.

Choisir une fonction de lien ?

Si le choix d'un unique indice de diversité peut paraître arbitraire par rapport au traitement des abondances des espèces, utiliser une relation linéaire, relier la similarité écologique et la mesure de distances l'est également. A priori, l'unique axiome raisonnable qu'on peut formuler pour caractériser cette fonction de lien est que la relation soit monotone et décroissante (et même dans ce cas des contre-exemples existent, par exemple dans le cas de convergence phylogénétique, où des espèces distinctes phylogénétiquement sont similaires écologiquement, WEBB et collab. [2002]).

LEINSTER et COBBOLD [2012] proposèrent en conséquence une fonction paramétrique liant la distance fonctionnelle ou phylogénétique à la mesure de similarité utilisée par l'indice de diversité. De la même façon que le paramètre q contrôle la perspective avec laquelle le patron de dominance est examiné, le paramètre de la fonction de lien contrôle la perspective avec laquelle la similarité entre espèces est examinée.

La fonction de lien qui a été utilisée dans cette thèse (Chapitre 2.1) est celle de PAGEL [1999]. Il proposa trois transformations paramétriques des longueurs des branches des phylogénies correspondant à différentes hypothèses évolutives pour modéliser adéquatement l'évolution d'un caractère. Celle que nous avons utilisée, la transformation δ, permet selon sa valeur de donner plus de poids aux longueurs de branches proches de la racine (si $\delta < 1$) ou proches des feuilles (si $\delta > 1$) ; en termes évolutifs, cela correspond respectivement à des hypothèses d'une évolution ancienne et d'évolution récente des traits (Figure 2.10). Pour $\delta = 0$, les longueurs de branches sont laissées inchangées. Si $\delta \to 0$, l'arbre se réduit à l'embranchement partant de la racine et toutes ses feuilles sont fusionnées en conséquence. Pour $\delta \to \infty$, tous les nœuds de l'arbre sont confondus avec la racine, l'arbre tend alors vers un arbre en étoile. Cette transformation offre donc une continuité intéressante entre la mesure de diversité incluant la similarité entre espèces et la diversité taxonomique considérant toutes les espèces également dissimilaires les unes aux autres (ce qui correspond à un arbre en étoile, $\delta \to \infty$).

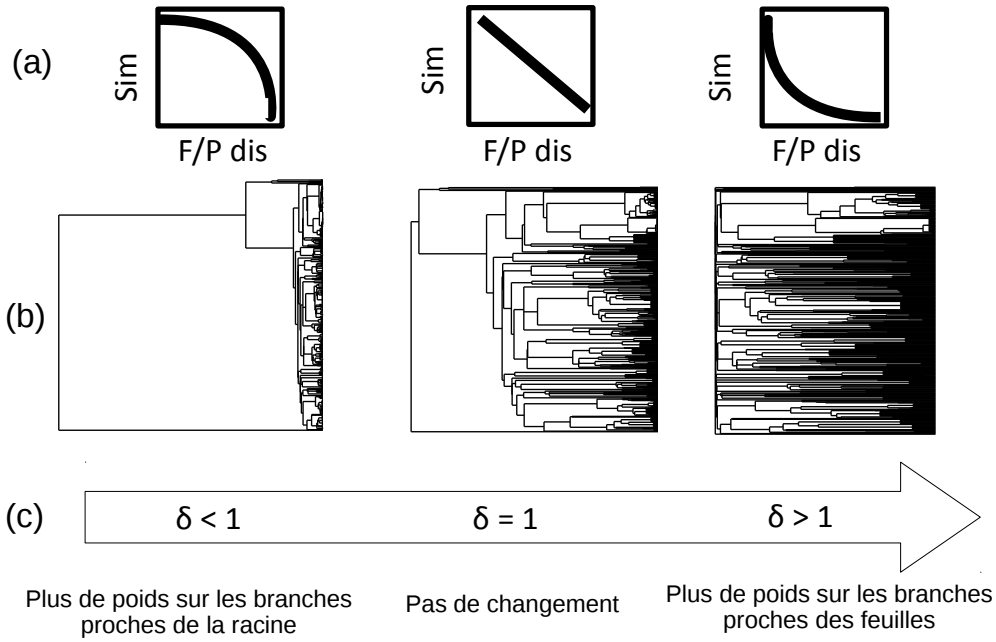

FIGURE 2.10 – Impact de la transformation de Pagel sur un arbre (b). La transformation est contrôlée par un paramètre δ (c) et implique la relation décrite en (a) entre distances fonctionnelles ou phylogénétiques (F/P dis) et similarité écologique entre espèces (Sim).

3 Plan du chapitre

Cette partie de la thèse est liée à mon travail sur les nombres de Hill et leur généralisation en diversités fonctionnelle et phylogénétique.

Le premier article (chapitre 2.1) porte sur la conception d'une analyse tirant parti de la généralisation des indices de diversité proposée par CHAO et collab. [2010] et de l'utilisation de la transformation d'arbres de Pagel décrite plus haut. Lors de cette étude, nous avons cherché à répondre aux questions : "Les patrons de diversité phylogénétique et fonctionnelle sont-ils influencés par la manière dont on prend en compte la dominance des espèces et le lien entre similarité écologique et distances phylogénétiques et fonctionnelles ?" et "Que cela nous apprend sur les règles d'assemblage des communautés végétales des Alpes ?"

Le deuxième article s'attache à proposer une décomposition multiplicative de la diversité phylogénétique et fonctionnelle en deux dimensions ayant les propriétés statistiques exposées par JOST [2007].

Le troisième article, auquel j'ai contribué en tant que coauteur, est une application de ces développements méthodologiques pour étudier les patrons de diversité α et β des communautés alpines et la manière dont ces derniers seront influencés par le changement du climat et d'utilisation des terres. N'ayant contribué que de façon mineure à cet

article, il est inclus en annexe.

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Chapitre 3

Effects of species' similarity and dominance on the functional and phylogenetic structure of a plant meta-community

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Effects of species' similarity and dominance on the functional and phylogenetic structure of a plant meta-community

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Abstract. Different assembly processes drive the spatial structure of meta-communities (β-diversity). Recently, functional and phylogenetic diversities have been suggested as indicators of these assembly processes. Assuming that diversity is a good proxy for niche overlap, high β-diversity along environmental gradients should be the result of environmental filtering while low β-diversity should stem from competitive interactions. So far, studies trying to disentangle the relative importance of these assembly processes have provided mixed results. One reason for this may be that these studies often rely on a single measure of diversity and thus implicitly make a choice on how they account for species relative abundances and how species similarities are captured by functional traits or phylogeny.

Here, we tested the effect of gradually scaling the importance of dominance (the weight given to dominant vs. rare species) and species similarity (the weight given to small vs. large similarities) on resulting β-diversity patterns of an alpine plant meta-community. To this end, we combined recent extensions of the Hill numbers framework with Pagel's phylogenetic tree transformation approach. We included functional (based on the leaf–height–seed spectrum) and phylogenetic facets of β-diversity in our analysis and explicitly accounted for effects of environmental and spatial covariates.

We found that functional β-diversity was high when the same weight was given to dominant vs. rare species and to large vs. small species' similarities. In contrast, phylogenetic β-diversity was low when greater weight was given to dominant species and small species' similarities. Those results suggested that different environments along the gradients filtered different species according to their functional traits, while, the same competitive lineages dominated communities across the gradients.

Our results highlight that functional vs. phylogenetic facets, presence-absence vs. abundance structure and different weights of species' dissimilarity provide complementary and important information on the drivers of meta-community structure. By utilizing the full extent of information provided by the flexible frameworks of Hill numbers and Pagel's tree transformation, we propose a new approach to disentangle the patterns resulting from different assembly processes.

Key words: alpine communities; β-diversity; community assembly; functional diversity; Hill numbers; phylogenetic diversity.

Introduction

The spatial structure of meta-community diversity (β-diversity) is a key feature for understanding how the environment shapes biodiversity patterns (Kraft et al. 2011, Myers et al. 2013). While evaluating the change in species identities and relative abundances across communities has a long tradition in community ecology (Cody and Diamond 1975), recent work has highlighted the value of studying the change in species ecological similarities instead, in order to identify the spatial patterns that emerge from different historical, ecological, and evolutionary processes (Graham and Fine 2008). In that perspective, distance measures applied to functional traits and phylogenetic trees have been increasingly used to estimate species ecological similarities (Pavoine and Bonsall 2011). Functional distances are based on species' functional traits, i.e., measurable morphological, physiological or phenological features that impact their fitness via their effects on growth, reproduction, and survival (Violle et al. 2007) and thus are directly connected to species' niches (Thuiller et al. 2004). Pairwise species' phylogenetic distances measure divergence times during evolutionary history and are often argued to be a good synthetic measure of species ecological differentiation as they do not require the identification and measurement of relevant traits (Faith 1992, Webb 2000, Mouquet et al. 2012).

However, functional and phylogenetic diversity do not necessarily provide similar information and patterns (Cadotte et al. 2013, Thuiller et al. 2014*b*). How strongly their patterns overlap depends on the strength of

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phylogenetic signal in the functional traits (i.e., the trend for closely related species to be more similar than distantly related species), which in turn depends on the underlying processes of niche evolution and species diversification (Losos 2008, Burns and Strauss 2011). The joint analysis of functional and phylogenetic facets of diversity can thus provide simultaneous hypotheses on the impacts of past evolutionary history (phylogenetic diversity) and specific phenotypic traits (functional diversity) on current ecological processes (Devictor et al. 2010, Safi et al. 2011, Cadotte et al. 2013).

If functional or phylogenetic similarities are suitable proxies for niche overlap then the observed patterns of β-diversity can shed light on the underlying ecological and evolutionary processes. High β-diversity along steep ecological gradients would identify a strong effect of ecological processes that foster the local co-occurrence of similar species and the regional differentiation of communities, suggesting either strong environmental filtering or dispersal limitation. Otherwise, very low β-diversity along steep ecological gradients reveals a stability of community structure, suggesting an absence of environmental filtering on the species feature studied, unlimited dispersion, or widespread local coexistence of competitive species (Spasojevic et al. 2014). These ecological processes are not exclusive and rather act simultaneously producing a complex pattern of diversity. We propose here that this complexity can be disentangled by gradually varying the effects of (1) species similarity and (2) species dominance in the functional and phylogenetic diversity patterns.

A pervasive, but never challenged, assumption in studies of community assembly is that species ecological similarity varies linearly with interspecific functional or phylogenetic distance (e.g., Webb 2000, Mason et al. 2005). However, this is done for reasons of simplicity and with little theoretical foundation as the scenario of trait evolution that would result in this linear relationship is unlikely (see, e.g., Fig. 3 in Thuiller et al. 2010). Studies on phylogenetic diversity patterns have shown that contrasted assembly processes can be detected when considering, for instance, all lineages of a metacommunity or only a specific lineage (Cavender-Bares et al. 2006, Münkemüller et al. 2014). It has been also suggested that competitive interactions could often be restricted to specific lineages or functional groups (Cavender-Bares et al. 2006, Slingsby and Verboom 2006), while environmental filtering could be predominant when considering the assembly of distantly related lineages (Vamosi et al. 2009), due to broad climatic adaptations being conserved in angiosperms lineages (Crisp et al. 2009). Modeling species ecological similarities by assuming that all parts of the phylogeny or functional tree (i.e., a dendrogram based on species trait dissimilarities) are equally relevant may thus hinder the detection of assembly processes operating between closely related species or functionally close species vs. highly dissimilar ones. Instead, varying the importance given to small compared to large species similarities (i.e., to branches close to the root vs. to branches close to the tips of the phylogenetic or functional tree) in the diversity patterns analysis may allow to uncover the different patterns at different similarity scales (called "similarity effect" hereafter).

Communities often exhibit an uneven species abundance distribution (Volkov et al. 2003). Usually a few species make most contribution to community biomass, vegetation cover or number of individuals while the majority of species are locally rare. Different ecological processes are responsible for this dominance pattern commonly observed (de Bello et al. 2012). Hierarchical scaling of community assembly rules (Lortie et al. 2004) and recent modeling developments have indeed hypothesized that while occurrence patterns may be primarily driven by environmental filtering, the local abundance of species mostly results from the interplay between biotic interactions and dispersal limitations (Boulangeat et al. 2012). We therefore expect that diversity patterns analyses yield contrasting results according to the importance given to dominant vs. rare species (called "dominance effect" hereafter).

The similarity and the dominance effects can impact the identification of patterns and the interpretation of underlying ecological processes and may thus be highly informative for our ecological understanding. However, in most diversity studies these effects are not explicitly considered. Instead, implicit weights are given to species similarities and abundance differences through the selection of an a priori diversity index (Tuomisto 2010*a*, Pavoine and Bonsall 2011). This lack of explicit consideration may be partly explained by the fact that comprehensive methods were unavailable so far. However, recent extensions of the Hill numbers (Hill 1973) now allow computing diversity indices with varying strength of the dominance effect, while at the same time considering species ecological dissimilarities (Pavoine et al. 2009, Chao et al. 2010, Leinster and Cobbold 2012). Additionally, studies of trait evolution have long used transformed trees to explicitly parameterize the importance of the phylogenetic similarity effect. One common tree transformation is the delta transformation (Pagel 1997). The rationale of this transformation is that a phylogenetic tree stretched close to the root puts more weight on large phylogenetic distances while a tree stretched close to the tips puts more weight on small phylogenetic distances. We use this approach to include and parameterize the strength of the similarity effect in our β-diversity analysis.

Here, we build on a multiplicative α, β, γ decomposition framework (Whittaker 1960, Jost 2007) in which we explicitly integrate the dominance and similarity effects into the study of functional and phylogenetic diversity patterns. Our study system is a plant metacommunity composed of 120 community plots in a valley of the French Alps. Our hypothesis is that interacting environmental filters and competition drive

the diversity patterns in these plant communities (Boulangeat et al. 2012). We ask whether the integration of the similarity and dominance effects allows us to identify diversity patterns that would have been hidden in a classical diversity analysis. More specifically, we test whether environmental filters can be detected based on β-diversity patterns that build on low dominance weights and strong weights on large species similarities and whether competition can be detected based on β-diversity patterns that build on high dominance weights and low weights on large species similarities. In addition we ask, whether trait diversity and phylogenetic diversity capture the expected patterns equally well.

Materials and Methods

Data

Study area.—The study area was the 25 km long Guisane Valley located in the center of the French Alps (~260 km^2; 44.9° N, 6.5° E). The valley is characterized by contrasted climatic conditions, with mean annual temperatures ranging from −8.1°C to 7.7°C. As in other valleys of the central Alps, the landscape is a mosaic of coniferous and deciduous forests, shrub heaths, subalpine grasslands and alpine meadows. All these habitats were represented in our data set.

Environmental data.—We used climatic variables (mean temperature of the coldest month of the year, relative summer wetness and sum of winter precipitations) and topographic variables (bedrock carbon content, topographic wetness index, and topographic position, i.e., topographic convexity or concavity). The climatic variables were originally extracted from the AURELHY database (Benichou and Le Breton 1987), downscaled to a 100-m resolution (Zimmermann et al. 2007), while the topographic variables came from a 50-m resolution digital elevation model.

Community plots.—We worked with a meta-community of 120 community plots that have been sampled in the Guisane valley from 2009 onward by the Alpine National Botanic Conservatory. Sites were representative of the heterogeneity of the valley's climatic conditions. They were on average separated by 10 km (only 0.4% of site pairwise geographic distances fell below the threshold of 100 m set by the climatic variables resolution). The herbaceous strata of the community-plots were surveyed within an approximate area of 100 m^2 of homogeneous vegetation by expert botanists. The abundance estimates were based on an abundance–dominance scale using six cover classes (Braun-Blanquet 1946). Our meta-community data set included initially a total of 531 species.

Functional tree.—We chose three functional traits that describe species' ecological strategies according to the leaf–height–seed spectrum: specific leaf area, height, and seed mass (LHS; Westoby 1998). These traits are strongly related to the fundamental processes of plant life, i.e., dispersal, establishment, and persistence (Weiher et al. 1999), and their combination has been useful to capture the existing variation in plant ecological strategies (Lavergne et al. 2003, Slingsby and Verboom 2006). Specific leaf area (SLA, i.e., light intercepting area per leaf dry mass) reflects the trade-off between resource acquisition and conservation in plants. Height at maturity is related to competitive ability and avoidance of environmental stress (Körner 2003). Seed mass strongly influences dispersal and is related to establishment (Pakeman et al. 2008). The trait information from each species was retrieved from the Alpine functional trait database (ANDROSACE; W. Thuiller et al., *unpublished data*). The database includes trait information for alpine plants from several in-house projects and freely available databases (see Appendix A for details). We excluded species for which less than two traits were available. The remaining 400 species still accounted for more than 80% of the total abundance of each studied community (Pakeman and Quested 2007). We then calculated the relative abundance of each species by dividing the abundance estimates by the total abundance of the remaining species in each community. Finally, we estimated the functional distance matrix from the trait-by-species matrix. Each trait was previously log-transformed to conform to normality and scaled between 0 and 1. We then constructed a functional tree as a prerequisite for performing the tree transformation detailed below. We used a hierarchical clustering approach to build an ultrametric functional dendrogram (functional tree; Mouchet et al. 2008) of all species, employing an average agglomeration method (UPGMA, function hclust in R).

Phylogenetic tree.—We used an ultrametric genus-level phylogeny of alpine plants extracted from Thuiller et al. (2014*a*) that followed the workflow proposed in Roquet et al. (2013) with DNA sequences downloaded from Genbank (see Appendix A for details). The tips of the phylogenetic tree were resolved with polytomies to obtain a species-level phylogeny. The 400 species were vascular plants, mostly angiosperms (393 species) but also included six ferns species and one spike moss species.

Analysis

We performed our analyses in three steps. First, we calculated how strongly trait values relate to the phylogenetic tree, for each single trait but also for all traits together (phylogenetic signal). Second, we tested the effects of similarity and dominance on the estimation of meta-community β-diversities (functional and phylogenetic). Finally, we tested the strength of the influence of space and environment on intercommunity pairwise diversities as a function of the similarity and dominance effects.

Phylogenetic signal in functional traits.—We used Pagel's λ (1997) to measure the strength of the phylogenetic signal of each functional trait. λ is a scaling parameter for the phylogeny. Its value is fitted so that the resulting transformation of the phylogeny ensures the best fit of trait data to the Brownian motion

model. If λ is not significantly different from 0, the trait distribution is independent from the phylogeny. We estimated λ with the function fitContinuous (R package geiger; Harmon et al. 2008) and tested it against the hypothesis that the trait distribution was independent from the phylogeny ($\lambda = 0$) using a log-likelihood ratio test (Münkemüller et al. 2012).

To test the phylogenetic signal of the LHS scheme (the three traits together), we performed a Mantel test between the matrix of the functional tree distances and the matrix of the square-root phylogenetic distances, as recommended by Hardy and Pavoine (2012).

Diversity decomposition and meta-community β*-diversity*.—We used the generalization of Chao et al. (2010) of Hill numbers (Hill 1973) to estimate the phylogenetic or functional α-diversity of each community and the γ-diversity of the whole meta-community. Following this generalization implies calculating a diversity index, which takes into account species similarities based on the branch lengths of either a phylogenetic or functional tree.

The index is a function of a parameter q, which varied between 0 and $+\infty$ and reflects the effect of dominance on the diversity estimation. The more q increases, the more ${}^qD$ is influenced by dominant species and the less by rare species

$$ {}^qD(p) = \begin{cases} \left(\sum_i \frac{L_i}{T} \times p_i^q \right)^{\frac{1}{1-q}} & q \neq 1 \\ \exp\left(-\sum_i \frac{L_i}{T} \times p_i \times \log(p_i) \right) & q = 1 \end{cases} \quad (1) $$

where the summation is over all branches of an ultrametric phylogenetic or functional tree of tips-to-root distance I, L_i is the length of branch i, and $p = \{p_i\}$ denotes the vector containing the summed relative abundance of all descendent species for each branch.

To calculate the α-diversity for each community, p was calculated from the vector of the relative abundance of the N species occurring in the community, while to calculate the γ-diversity of the meta-community, p was calculated from the vector of the average relative abundance of the species over all communities (i.e., the entire meta-community). To improve the computational efficiency of our analysis, we used the mathematical formulation of ${}^qD$ given in the appendices of Leinster and Cobbold (2012; R function available in Supplement 1).

Additionally, in Appendix B, we adapted the inclusion of species' similarity to an alternative generalization of Hill's number proposed by Leinster and Cobbold (2012) that relies on slightly different calculations (i.e., based on similarity matrices instead of trees). We compared the output of the two approaches and showed that they revealed largely similar results (see Appendix B for these analyses and discussion of relative advantages of both approaches).

Characteristics of the applied diversity measure.—The diversity measure we used here is strongly related to other well-known measures. If species are considered to be equally similar (i.e., they are linked by a star-like tree), then ${}^qD$ (1) is equal to the number of species for $q = 0$, (2) tends toward the Shannon entropy exponential for q tending toward 1, and (3) is the inverse of Simpson for $q = 2$.

If species are not considered equally similar, then ${}^qD$ is equal (1) to Faith index for $q = 0$ (Faith 1992), (2) to the exponential of Allen's index for q tending toward 1 (Allen et al. 2009), and (3) to a monotonic transformation of Rao's quadratic entropy, for $q = 2$ (Rao 1986).

The effects of similarity were taken into account using a transformation of the functional and phylogenetic trees of the entire Guisane meta-community prior to calculating diversity indices. We influenced the effect of similarity using the delta transformation of trees proposed by Pagel (1997) in a phylogenetic context (Appendix B: Fig. B1). The delta transformation raises the depth of the tree nodes to the power of δ. In concrete terms, it inflates (respectively deflates) the length of close-to-root branches compared to close-to-tips branches when the parameter δ is lower (respectively higher) than 1. When δ tends toward $+\infty$, i.e., the transformed tree tends toward a star-like tree, all species are considered equally similar, and the diversity index approaches a measure of taxonomic diversity. In contrast, when δ tends toward 0, the transformed tree is reduced to the two branches descending from the root and species are fused together according to this branching.

In species similarity terms, the delta transformation allows playing with the effect of similarity between species and shifts the scope of the analysis from large species cophenetic distances (weak similarity effect, $\delta < 1$) to small species cophenetic distances (strong similarity effect, $\delta > 1$, Appendix B: Fig. B1).

All together, we thus computed γ-diversity and α-diversity using a function that depended on both the similarity (δ) and the dominance (q) effects.

Meta-community β*-diversity standardized effect sizes*.—β-diversity was calculated as the ratio of γ-diversity and the average α-diversity of the meta-community estimated as the generalized mean of degree $1 - q$ of the α-diversities of all communities (Jost 2007, Tuomisto 2010*a*, Chiu et al. 2014)

$$ \beta(q,\delta) = \begin{cases} \gamma(q,\delta) \Big/ \left[\frac{1}{S} \sum_j^S \alpha_j(q,\delta)^{1-q} \right]^{\frac{1}{1-q}} & q \neq 1 \\ \gamma(q,\delta) \Big/ \exp\left[\frac{1}{S} \sum_j^S \log\left(\alpha_j(q,\delta) \right) \right] & q = 1 \end{cases} \quad (2) $$

with α_j the α-diversity of community j and S the number of communities.

β has a minimal possible value of 1 if all communities are identical in species abundances and species identities. Furthermore, ${}^{q}D$ obeys the replication principle. This means that if the studied communities had all an equal α-diversity, if they did not have any species in common, and if the species belonging to different communities are descending from different functional or phylogenetic tree branches, then the $\beta(q, \delta)$ of the study area would be maximized and equal to S (Chiu et al. 2014). The replication principle is a necessary condition for the independence of α and β and is thus essential to obtain meaningful measures of β-diversity (sensu Jost 2007).

The value of $\beta(q, \delta)$ was then tested against a null model of tip-shuffling to access whether the observed β-diversity was higher or smaller than expected from a model of random assembly of the species from the meta-community pool. We then calculated the standardized effect size (SES) of the β-diversity as the mean of the distribution minus the observed β-diversity divided by the standard deviation of the null distribution. If the β-diversity was higher than expected (SES < 0) then the communities differed more than expected under a random assembly model; if the β-diversity was lower than expected (SES > 0), then the communities differed less than expected under a random assembly model.

Influence of environment and space on intercommunity pairwise functional and phylogenetic diversities.—Similarly to strong environmental filtering, dispersal limitation and ecological drift can also result in high β-diversity among communities (Ricklefs 2008). In this case, we can expect the intercommunity pairwise functional and phylogenetic diversities pattern to be spatially auto-correlated. In order to avoid any misinterpretation of diversity patterns, which may be partially influenced by these confounding processes, and to fully characterize the fingerprint of environmental filtering, we explicitly linked the intercommunity pairwise functional and phylogenetic diversities to environmental variables and space following a procedure based on Dray et al. (2012).

We then developed an approach to disentangle the relative effects (and their interaction) of space and environment on the structure of communities. To do so, we first defined space with Moran's eigenvector maps (MEM) based on a Gabriel graph obtained from the sites geographical coordinates. We retained only the MEMs with significant Moran's I ($P < 0.05$). To define environment, we performed a principal component analysis (PCA) on environmental variables and extract sites scores along all the PCA axes. Second, for both phylogenetic and functional information, we generated intercommunity pairwise diversities matrices in function of the q and δ parameters by calculating the functional and phylogenetic β-diversities (Eq. 2) between all pairs of communities. We subtracted 1 (the minimal possible value) from each diversity value to build a matrix of intercommunity pairwise diversities corresponding to the Whittaker's effective species turnover (Whittaker 1960, Tuomisto 2010*b*). Third, we performed a principal coordinates analysis (PCOA) to separate the communities in a multivariate space and extract community scores along the PCOA axes. We then applied a forward selection procedure to the MEM spatial predictors to retain the most relevant spatial predictors for each intercommunity pairwise diversities matrix (phylogenetic and functional, for each pair of q and δ; Blanchet et al. 2008). Finally, to partition the importance of space and environment to explain patterns of intercommunity pairwise diversities, we performed a variance partitioning procedure on the matrices of site scores deduced from the PCOA, with the matrix of relevant MEM and the matrix of site scores along the axes of the PCA on environmental variables as cofactors (Borcard et al. 1992). We therefore obtained for each pair of q and δ parameters and each diversity facet (functional and phylogenetic), the variance explained by environment after controlling for space ($E\backslash S$), the variance explained by space after controlling for environment ($S\backslash E$) and the variance explained by the interaction of space and environment ($S \times E$). These explained variances were defined as adjusted R^2.

All analyses were carried out using the software R 3.0.1 (R Development Core Team 2013) with the packages ade4, ape, geiger, packfor, snowfall, spacemakeR, spdep, and vegan.

Results

Phylogenetic signal of functional traits

All the individual traits exhibited a significant phylogenetic signal. SLA and height had moderate values of λ (height, $\lambda = 0.52$, $\chi^2 = 70.54$, df $= 1$, $P < 0.001$; SLA, $\lambda = 0.56$, $\chi^2 = 35.99$, df $= 1$, $P < 0.001$). Seed mass had the strongest phylogenetic signal (seed mass, $\lambda = 0.97$, $\chi^2 = 249.95$, df $= 1$, $P < 0.001$). The phylogenetic signal of the species LHS scheme was significant but very low (Mantel test, $R^2 = 0.06$, $P < 0.001$).

Meta-community β-diversity standardized effect sizes

The standardized effect sizes (SES) of functional β-diversity were overall low, but more specifically (SES < -3) for low values of q ($q < 1$) or for low to intermediate values of δ ($0.02 < \delta < 4$, intermediate similarity effect, Fig. 1A). For more extreme values of δ ($\delta < 0.2$ or $\delta > 2$) and high values of q ($q > 5$), SES increased and the functional pattern of β-diversity became not discernible from the random expectation (SES > -2 and SES < 2). Overall this suggested a predominant influence of environmental filtering on functional diversity both when the dominance effect was weak (i.e., all species present have equal weight) and when the similarity effect was moderate (i.e., approximately unchanged functional tree branch lengths).

When focusing on phylogenetic diversity, the pattern was radically different and more complex (Fig. 1B). In general, SES of the meta-community phylogenetic β-diversity was lower than for functional diversity. Like

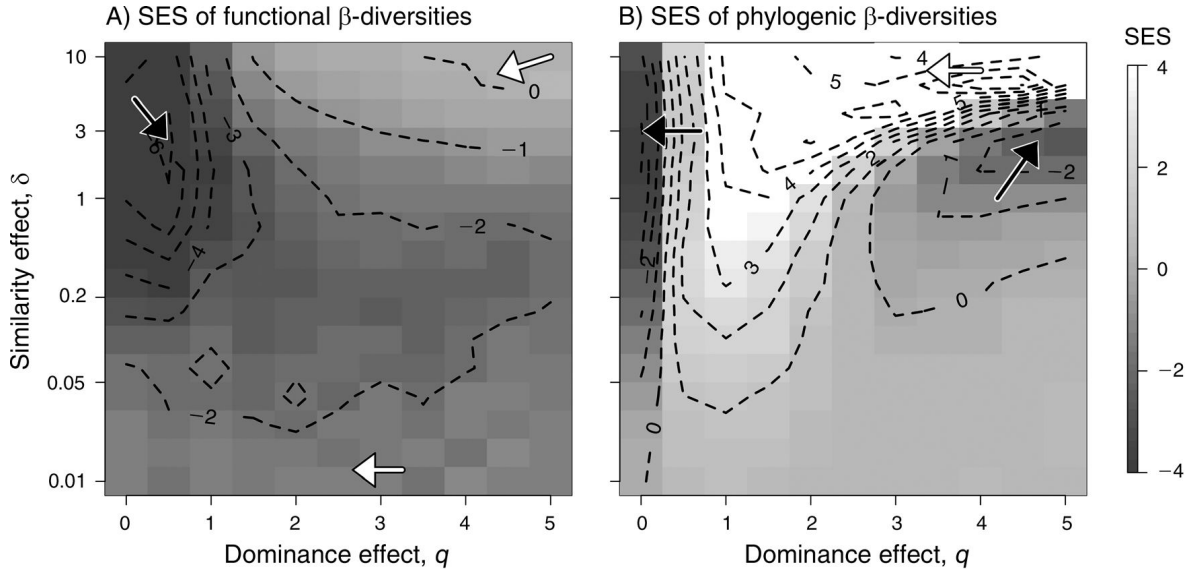

FIG. 1. Standard effect sizes (SES) of the (A) functional and (B) phylogenetic β-diversity of the meta-community against a tip-shuffling null model, as a function of the strength of the dominance effect (q) and the strength of the similarity effect (δ). A low q value indicates that rare and dominant species were given about the same weight while a high q value indicates that more weight was given to dominant species. A low (respectively high) δ value indicates that small (respectively large) species' similarities were given more weight. A low SES value indicates a higher than expected β-diversity, hence a predominant influence of environmental filtering, while a high SES value indicates a lower-than-expected β diversity, hence a predominant influence of competition. Black and white arrows points toward local minima and maxima, respectively.

the functional β-diversity, the phylogenetic β-diversity was noticeably low (SES < -3) for low values of q ($q < 0.5$). However, the β-diversity was noticeably high (SES > 3) when q was between 0.8 and 2 or when δ was higher than 3. Otherwise the β-diversity did not differ strongly from the null expectation (SES > -2 and SES < 2). Overall, this suggested that communities had a similar phylogenetic structure under a moderate dominance effect and when small phylogenetic distances were emphasized ($\delta > 3$). When the dominance effect was reduced or ignored ($q < 0.5$), we detected environmental filtering, while we detected a random assembly process when considering a strong dominance effect.

Effects of environment and space on intercommunity pairwise diversities

The second analysis yielded similar results as the first one and mainly confirmed that the functional β-diversity pattern was indeed driven by the strong environmental gradients of the Guisane valley.

The purely environmental component (E/S) explained only a small portion of the variance of the functional and phylogenetic intercommunity pairwise diversities regardless of the dual effects of dominance and similarity ($R^2 < 0.10$; Fig. 2A and D).

The environmental component interacting with space ($S \times E$) explained a variable proportion of the intercommunity pairwise functional diversities depending on the strength of the dominance and similarity effect (Fig. 2B). A moderate amount of variation was explained for functional diversity for a weak dominance ($q < 2$) or a moderate similarity effect ($0.5 < \delta < 4$) with a maximal adjusted R^2 of 0.20 (for $q = 1$ and $\delta = 1.58$). In comparison with the functional diversity pattern, the environmental component interacting with space ($S \times E$) explained overall a low amount of variation of the phylogenetic diversity (Fig. 2E) with a mean adjusted R^2 of 0.04.

The purely spatial component (S/E) explained overall a moderate proportion of the variance in the intercommunity pairwise functional diversities with a mean adjusted R^2 of 0.12. The purely spatial component (S/E) explained overall a moderate proportion of the variance in the intercommunity pairwise phylogenetic diversities matrices with a mean adjusted R^2 of 0.19. It, however, reached high values of adjusted R^2 for a weak dominance and similarity effect ($\delta < 0.2$, $q < 0.5$) with a maximal adjusted R^2 of 0.73 (for $q = 0$ and $\delta = 0.01$). More in-depth analyses revealed that this combination tended to distinguish particular communities (mostly marshes) that contained species from the long branches of our phylogeny (spike moss and fern species) from the angiosperms. As these species were both infrequent and locally rare, their contribution was masked when the dominance and similarity effect were strong.

DISCUSSION

The strong environmental gradients in alpine ecosystems are known to be important drivers of community structure (Mitchell et al. 2009, de Bello et al. 2012). In observational field studies, they are often the only identified drivers whereas local experiments demonstrated the importance of positive and negative biotic interactions between plant neighbors (Choler et al.

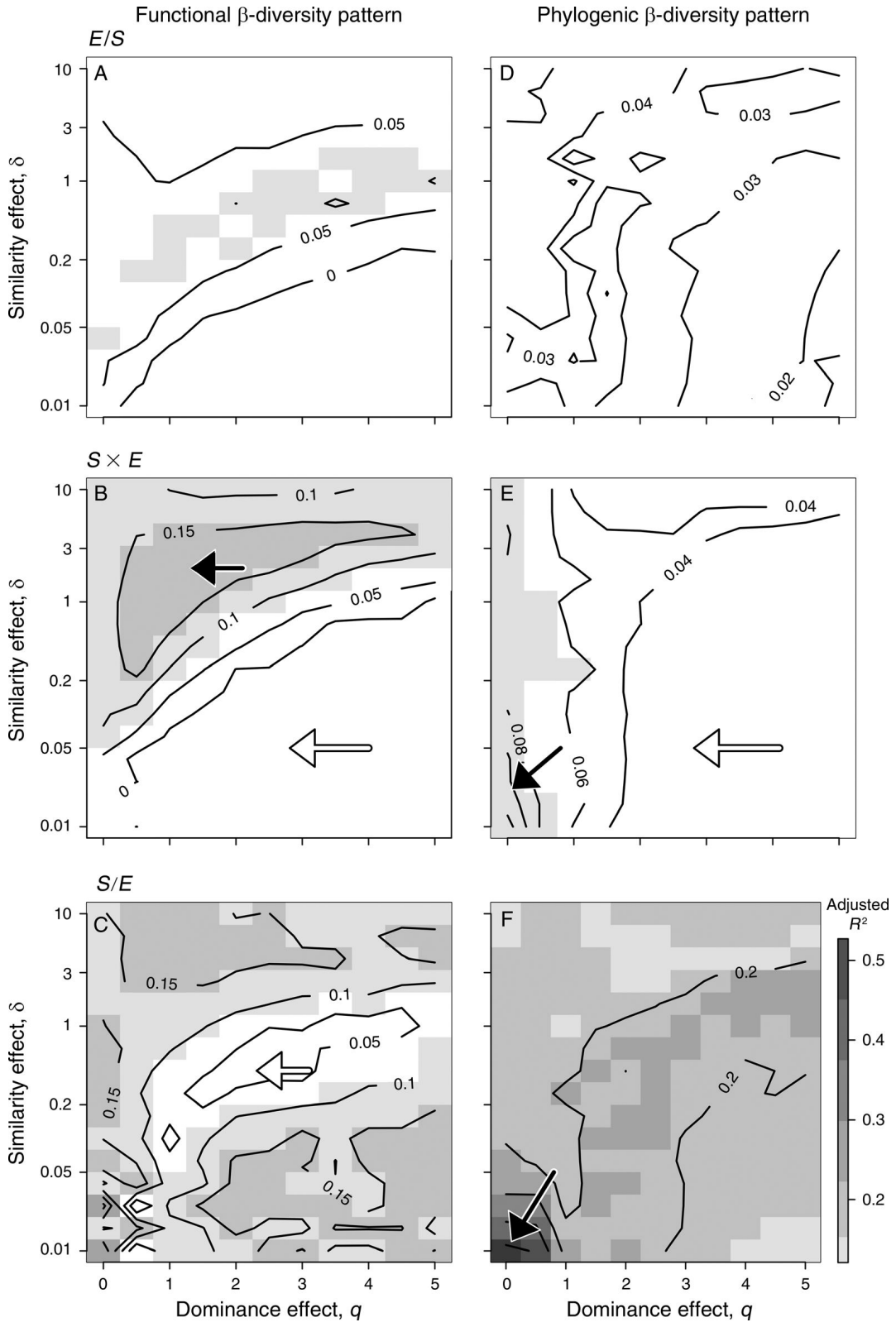

FIG. 2. Influence of environment (E) and space (S) on the intercommunity pairwise functional and phylogenetic diversities, as a function of the strength of the dominance effect (q) and the strength of the similarity effect (δ). A low q value indicates that rare and dominant species were given about the same weight while a high q value indicates that more weight was given to dominant species. A low (respectively high) δ value indicates that small (respectively large) species' similarities were given more weight (Fig. 1). The different lines and shades of gray represent the variance (adjusted R^2) of the matrix of intercommunity pairwise diversities explained by environment only (E/S), spatially autocorrelated environment ($S \times E$) and a pure spatial effect (S/E). Black and white arrows points toward local maxima and minima, respectively.

2001, Callaway et al. 2002). This apparent discrepancy is rooted in the fact that most published studies have either focused on functional or phylogenetic diversity and have chosen, or implied, a single arbitrary dominance and similarity effect. Here we show that jointly investigating both functional and phylogenetic patterns together with a comprehensive inclusion of dominance and similarity effects can reveal multiple patterns likely due to either environmental filtering or negative biotic interactions.

Variable composition and stable phylogenetic dominance structure across communities

Patterns of functional and phylogenetic β-diversity were very different in the study region. This mismatch stemmed in the moderately low phylogenetic signal of the functional traits studied both taken individually and together. As a consequence, the two facets of diversity appeared quite decoupled in the study meta-community. Assuming that species' niches can be abstracted as multidimensional hypervolumes (Hutchinson 1959), functional traits and phylogenetic identity can thus be interpreted as surrogates of distinct niche dimensions.

Interestingly, our analyses suggested that environmental filtering was the main driver of the patterns of functional and phylogenetic β-diversity when rare and dominant species were given the same weight (Figs. 1 and 2). This suggested that the functional and phylogenetic compositions of the communities were filtered out by the strong abiotic gradients of the Guisane valley (albeit quite weakly for the phylogenetic identity of species, Fig. 2D and E).

However, for a stronger dominance effect, the imprint of environmental filtering was less pervasive on the functional β-diversity. More strikingly, the observed phylogenetic β-diversity was consistently low relative to random expectations, suggesting a high stability of the phylogenetic community structure across space. This was true only when the similarity effect was strong ($\delta > 1$), i.e., when small phylogenetic similarities were given more weight. We interpreted this pattern as the consequence of the dominance of some angiosperms lineages over other lineages in alpine herbaceous communities. For a weak similarity effect (thus when angiosperms species are considered highly similar), the pattern of phylogenetic stability of dominant angiosperms lineages was blurred by the random turnover of non-angiosperms vs. angiosperms between communities.

These last results showed that while communities differed strongly in terms of functional traits, their dominant species tended to come from the same lineages, suggesting a strong competitive advantage. In other words, the leaf–height–seed strategy scheme (Westoby 1998) was mainly informative about environmental filters driven by climatic gradients. Thus communities strongly varied along the gradients in regard of the trait values of their constituent species (Figs. 1A and 2B). Conversely, species phylogenetic differences informed weakly about environmental filters (Fig. 2D and E) supporting other local diversity patterns studies (Silvertown et al. 2006, Bernard-Verdier et al. 2013). However phylogenetic β-diversities seemed to capture niche information related to competitive hierarchy suggesting that competition was driven by unmeasured traits showing potentially strong phylogenetic signal.

Both the study of β-diversity SES and intercommunity pairwise diversities yielded similar results about the action of environmental filtering on the functional and phylogenetic β-diversity patterns. The covariation of the intercommunity pairwise functional β-diversities with environmental variables suggested that the functional high β-diversity was driven by the steep local environmental gradients and was not solely due to spatial autocorrelation effects or to confounding assembly processes (Mayfield and Levine 2010). Our results further emphasized that the functional and phylogenetic β-diversity patterns were spatially auto-correlated; in particular within a specific window (low δ and q) for the phylogenetic diversity pattern. Our study area encompasses a single valley of limited area (260 km^2) suggesting little influence of ecological drift. We thus associated the spatial autocorrelation to the influence of dispersal limitation or spatially structured environmental gradients that we did not directly account for.

The dominance effect had an important impact on the detection of diversity patterns. When the dominance effect was weak, our results suggested a more pervasive print of environmental filtering (Figs. 1A and 2) while for a strong dominance effect, communities seemed to be more driven by stochastic processes (in regard of the functional traits we studied) and competition (in regard of their phylogenetic identity; Fig. 1). We hypothesized that the environmental filters along the Guisane valley gradients primarily influenced which traits allowed species establishment within communities, but not which traits shaped species' competitive hierarchies. In contrast, environmental gradients did not strongly influence the phylogenetic community structure. Regardless of the location along the gradients, the communities were structured by a few dominant species from the same lineages (e.g., Poaceae, Fabaceae, Asteraceae). In combination, these two patterns suggested that these lineages maintain their dominance across environmental gradients thanks to strong trait lability, which has allowed (1) trait convergence and thus coexistence of distantly related species into communities despite strong environmental filters (Webb 2000) (2) the within-lineage emergence of niche-segregated species sorted out along gradients (Angert and Schemske 2005).

The similarity effect interacted with the dominance effect to reveal hidden features of the diversity patterns. The intercommunity pairwise functional distances were more strongly linked to environment for a moderate similarity effect, i.e., when the functional tree branch lengths were almost unchanged (Fig. 1). However, a weak or a strong similarity effect hinder the detection of

an environmental effect showing that tree branch transformation was unsuitable to improve the understanding of community assembly along environmental gradients.

To summarize, the presence–absence structure of communities was mainly driven by the high turnover of species due to the environmental filtering of their traits and phylogenetic identity while the dominance structure was mainly driven by the high abundance of the same lineages over the gradient, likely because of unmeasured competitive advantages.

Emphasizing the different features of meta-communities

Our results emphasize the importance of studying together different types of diversity as the interpretation of diversity patterns changed according to the studied diversity. In that perspective, the family of Hill numbers and its extension to phylogenetic and functional distances provides a promising framework to analyze the spatial patterns of meta-communities (Arroyo-Rodriguez et al. 2013). It allows fine-tuning of the effect of dominance and similarity, while retaining indices with similar mathematical properties (Chiu et al. 2014). Our results are particularly striking, since the parameterization drastically changed the detection of functional and phylogenetic diversity patterns. In return, this allowed us to suggest that different ecological processes affected the occurrence of species (low q values) and the local dominance of species (higher q values), as also found in Boulangeat et al. (2012). The similarity effect tended to reveal hidden patterns, in particular for the phylogenetic β-diversity pattern by either putting the emphasis on ancient or recent species' divergences.

There are numerous discrepancies in the literature about the link between community assembly and functional or phylogenetic diversities. Among others, some functional traits can be associated to both environmental filtering and biotic interactions even in the same ecosystem (e.g., Gross et al. 2009, de Bello et al. 2012) and phylogenetic diversity has been associated to various patterns of diversity (Mouquet et al. 2012). While spatial or evolutionary scale have been proposed to explain these various outcomes (Cavender-Bares et al. 2009), the impact of giving the same weight to all parts of the functional or phylogenetic tree is rarely tested (Thuiller et al. 2010, Cadotte et al. 2013). We argue here that the inclusion of the similarity effect in diversity patterns studies may help to clarify these discrepancies and provide more complete, if not clearer, diversity patterns. Other studies have done a similar job either through null model modifications (Hardy and Senterre 2007, Chalmandrier et al. 2013) or through other types of tree transformations (Rosauer et al. 2013). However, these frameworks ignored the parts of the functional and phylogenetic trees close to the root (which correspond to a moderate to a strong similarity effect) while ours can also do the reverse procedure and ignore the close-to-tips parts of the trees (weak similarity effect). Taken together, the exploration of the dominance and similarity effect can help to determine the window in which the diversity pattern is best predicted by variables such as environment and space (Fig. 2), opening promising avenues to optimize the calibration of models of community turnover over space and environmental gradients (e.g., Dray et al. 2012, Rosauer et al. 2013).

Conclusion

The diversity patterns of meta-communities are the outcome of complex interactions between past evolution, current trait states, and multiple assembly rules (Cavender-Bares et al. 2009, Lavergne et al. 2010). Using an integrative framework of diversity pattern analysis, we demonstrated how the consideration of the dominance structure of communities and species ecological similarity affects diversity patterns of alpine plant meta-community. We found that environment controlled the functional and (more modestly) the phylogenetic diversity of the meta-communities when focusing on presence-absence like patterns (i.e., low dominance effect), which is typical of a compressed environmental gradient. Additionally, considering phylogenetic diversity in our innovative framework allowed us to suggest that biotic interactions shaped the dominance pattern. Together these results let us to conclude that alpine plant species have both labile functional traits to adapt to environmental gradients and unknown evolutionary conserved traits that drive community assembly via inter-specific competition. Explicitly testing the effects of dominance and species ecological similarity can thus help disentangling the multiple assembly rules affecting the functional and phylogenetic structure of meta-communities along environmental gradients.

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Supplemental Material

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Chapitre 4

Decomposing changes in phylogenetic and functional diversity over space and time

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Decomposing changes in phylogenetic and functional diversity over space and time

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Summary

1. The α-, β-, γ-diversity decomposition methodology is commonly used to investigate changes in diversity over space or time but rarely conjointly. However, with the ever-increasing availability of large-scale biodiversity monitoring data, there is a need for a sound methodology capable of simultaneously accounting for spatial and temporal changes in diversity.

2. Using the properties of Chao's index, we adapted Rao's framework of diversity decomposition between orthogonal dimensions to a multiplicative α-, β-, γ-decomposition of functional or phylogenetic diversity over space and time, thereby combining their respective properties. We also developed guidelines for interpreting both temporal and spatial β-diversities and their interaction.

3. We characterized the range of β-diversity estimates and their relationship to the nested decomposition of diversity. Using simulations, we empirically demonstrated that temporal and spatial β-diversities are independent from each other and from α- and γ-diversities when the study design is balanced, but not otherwise. Furthermore, we showed that the interaction term between the temporal and the spatial β-diversities lacked such properties.

4. We illustrated our methodology with a case study of the spatio-temporal dynamics of functional diversity in bird assemblages in four regions of France. Based on these data, our method makes it possible to discriminate between regions experiencing different diversity changes in time. Our methodology may therefore be valuable for comparing diversity changes over space and time using large-scale data sets of repeated surveys.

Key-words: β-diversity, biodiversity, phylogenetic entropy, Shannon entropy, Hill numbers, diversity partitioning, bird assemblages, large-scale monitoring, turn-over

Introduction

Patterns of species diversity, as determined by their functional traits and phylogenetic relationships, have become central to addressing a large range of research questions such as the inference of assembly rules in community ecology (Diamond 1975; Webb 2000; Mouquet *et al.* 2012) or the delimitation of biodiversity hotspots in macro-ecology (Mazel *et al.* 2014). Using functional and phylogenetic diversity indices implicitly rejects the assumption that species are equally distinct entities, and instead accounts for their functional similarities and shared evolutionary history (Violle *et al.* 2007; Mouquet *et al.* 2012).

Thanks to the extension of large-scale biodiversity monitoring (Pereira & Cooper 2006) and the development of citizen science (Bonney *et al.* 2009), large data sets have been made available for investigating the spatial and temporal dynamics of biodiversity (Dornelas *et al.* 2014). These are of prime importance in evaluating how species assemblages are responding to ongoing changes in climate and land uses. Since these temporal changes are not necessarily homogeneous across space, a depiction of biodiversity changes from both a spatial and temporal perspective (Magurran *et al.* 2010) is required to understand which processes contribute to biodiversity dynamics. An adequate methodology is therefore needed to produce meaningful measures of diversity changes over space and time.

In his seminal paper, Whittaker (1960) proposed breaking the regional species diversity (γ-diversity) down into the average within-community species diversity (α-diversity) and the between community species diversity (β-diversity). More specifically, Whittaker formulated two laws to link α, β and γ-diversities: an additive law ($\gamma = \alpha + \beta$) and a multiplicative law ($\gamma = \alpha \times \beta$). Two decomposition frameworks emerged from these two alternative approaches, each with different properties and drawbacks.

The additive law was adapted by Rao (1986) to the 'Quadratic Entropy' index which generalized the Gini–Simpson index to include species dissimilarities such as functional or phylogenetic distances. He further proposed decomposing γ-diversity into several dimensions (e.g. space and time), a procedure called *Anodiv* (Pavoine 2012). However, the additive decomposition of the γ-diversity, and by extension the *Anodiv* procedure, has been criticized for its inability to

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produce β-diversity estimates independent from the γ- and α-diversities (Jost 2007; Baselga 2010). This property impedes *Anodiv's* ability to access temporal or spatial biodiversity changes on large spatial scales. Indeed, large-scale biodiversity monitoring typically covers numerous regions with variable γ- and α-diversities (e.g. Devictor *et al.* 2010), a consequence of the large-scale environmental filtering and historical contingencies that shape the biogeographical gradients of diversity (Hawkins, Porter & Diniz-Filho 2003). Should β-diversities be compared across regions, it is vital that they only quantify spatial or temporal change within these regions, independently from changes in γ and α-diversities. Otherwise these two effects would become indistinguishable.

The second framework, based on Whittaker's multiplicative law, addresses this issue of independence. When diversity is calculated from an equivalent number (Hill 1973), it produces estimates of β-diversity which are independent from the α- and γ-diversities (Jost 2007; Tuomisto 2010). Furthermore, the estimate of the β-diversity is set between 1 and the number of communities in the region studied. This property makes it possible to produce standardized estimates of β-diversity which are not dependent on the study design used in the region (Chao, Chiu & Hsieh 2012). This is a particularly important feature since large-scale biodiversity monitoring systems tend to be spatially unbalanced (Ficetola *et al.* 2013). However, despite these properties, Whittaker's multiplicative law was never adapted to breaking functional or phylogenetic diversity down into different dimensions.

We have built on these two frameworks and their respective advantages to propose a novel methodology for decomposing phylogenetic and functional diversity over space and time, and obtaining measurements of β-diversity which are independent of γ-diversity and α-diversity. This study first introduces our multiplicative framework for estimating spatial and temporal beta diversities. Secondly, using a simulation-based approach, we demonstrate that in the case of taxonomic diversity, the estimated β-diversities are pairwise independent from the γ- and α-diversity and from each other. Finally, we illustrate its novelty and features in a case study by decomposing the spatio-temporal effects on the functional diversity of the common avifauna in four regions of France over the last decade.

Decomposing diversity over space and time

DEFINITIONS

We considered a region containing S sites in which species were recorded at T dates. We defined a community as the species composition of site s at a given date t. We defined a site pool as the pool of all communities at site s pooled for all dates, a time pool as the pool of all communities at a given date t pooled for all sites and the regional pool as the pool of all communities for all sites and dates. The spatio-temporal decomposition of diversity (multiplicative α-, β-, γ-decomposition) will ultimately be calculated based on the ratios of the diversities in these different units (communities and pools).

DIVERSITY INDEX

To calculate the diversity of a given unit, we used Shannon entropy exponential. This index is an 'equivalent number', part of the family of Hill numbers (Hill 1973). As such, its value ranges from 1 (if one species makes up most of the total abundance in the unit) to the number of species in the unit (if their relative abundances are all equal). It can be interpreted as the number of 'equally abundant virtual species' in the unit (Tuomisto 2010):

$$D(P) = \exp\left(-\sum_{i=1}^{N} \log(p_i) \times p_i\right) \qquad \text{eqn 1}$$

with P, the vector $\{p_1, p_2, \ldots, p_N\}$ of abundances of the N species present in the unit studied.

To include functional and phylogenetic similarities between species, we used the version of this index formulated by Chao, Chiu & Jost (2010) from Allen's phylogenetic entropy (2009).

$$D(P) = \exp\left(-\sum_{b} \frac{L(b)}{T} \log(p_B(b)) \times p_B(b)\right) \qquad \text{eqn 2}$$

where the summation is made over all branches of an ultrametric phylogenetic or functional tree of tips-to-root distance T, $L(b)$ is the length of branch b and p_B denotes the vector containing for each branch b, the summed relative abundance of its descendent species. We will refer to this index as Chao's index.

Since the index includes species similarities, its absolute value can be interpreted as the number of 'equally abundant and fully distinct virtual species' in the study unit.

SPATIO-TEMPORAL DECOMPOSITION

We drew inspiration from the *Anodiv* procedure (Rao 1986; Pavoine 2012) to decompose diversity according to two orthogonal factors, here time and space, according to a multiplicative framework using Chao's index. It is expressed as follows:

$$\begin{aligned} D(P..) = {} & \frac{D(P..)}{\exp\left[\sum_{t=1}^{T} \omega_t \times \log(D(P.t))\right]} \\ & \times \frac{D(P..)}{\exp\left[\sum_{s=1}^{S} \omega_s \times \log(D(Ps.))\right]} \\ & \times \frac{\exp\left[\sum_{t=1}^{T} \omega_t \times \log(D(P.t))\right] \times \exp\left[\sum_{s=1}^{S} \omega_s \times \log(D(Ps.))\right]}{D(P..) \times \exp\left[\sum_{t=1}^{T}\sum_{s=1}^{S} \omega_{st} \log(D(P_{st}))\right]} \\ & \times \exp\left[\sum_{t=1}^{T}\sum_{s=1}^{S} \omega_{st} \log(D(P_{st}))\right] \end{aligned} \qquad \text{eqn 3}$$

P_{st} is the vector of species relative abundance in community at site s and date t. The formulation includes ω_{st}, a weight

attributed to a community at site s and time t, that sums to 1 over all s and t based for instance on total abundance or species richness in the community. A perfectly balanced design will involve the absence of missing data and the equal weighting of all communities, that is for all s and t, $\omega_{st} = \frac{1}{ST}$. Unequal weighting is not compulsory but is typically relevant when communities have been sampled with different sampling efforts (for a discussion, see Hardy & Jost 2008).

ω_s and ω_t are the weights of site pools s and time pools t, respectively, and are calculated as the sum of the weights of their constituent communities. The vector of species relative abundance for the site pool s and time pool t is thus calculated as the weighted mean of the species relative abundances in their constituent communities: $P_{.t} = \frac{1}{\omega_t}\sum_{s=1}^{S}\omega_{st}P_{st}$ and $P_{s.} = \frac{1}{\omega_s}\sum_{t=1}^{T}\omega_{st}P_{st}$. Finally, the vector of species relative abundances in the species pool is calculated as the weighted mean of species relative abundance across all communities: $P_{..} = \sum_{s=1}^{S}\sum_{t=1}^{T}\omega_{st}P_{st}$.

Equation 3 can be reformulated as:

$$\gamma = \frac{\gamma}{\alpha_T} \times \frac{\gamma}{\alpha_S} \times \frac{\alpha_S \times \alpha_T}{\gamma \times \alpha} \times \alpha \qquad \text{eqn 4}$$

with γ being the γ-diversity of the study region; with α_T and α_S being, respectively, the mean α-diversity of time and site pools and α the mean α-diversity of the communities in the study region.

Or more simply,

$$\gamma = \beta_T \times \beta_S \times \beta_{ST} \times \alpha \qquad \text{eqn 5}$$

with β_T being the temporal β-diversity, β_S the spatial β-diversity and β_{ST} the interaction term between the temporal and the spatial β-diversities. If the spatial and temporal structure of the data set is ignored, the total β-diversity β of the region across time can be expressed as:

$$\beta = \frac{\gamma}{\alpha} = \beta_T \times \beta_S \times \beta_{ST} \qquad \text{eqn 6}$$

PROPERTIES OF THE β-DIVERSITIES

Chiu, Jost & Chao (2014) demonstrated that Chao's index obeyed the 'replication principle'. This implies that β_T and β_S have several of the properties enumerated in Jost (2007) and Tuomisto (2010), which facilitate the interpretation of their numerical values:

1. β_T and β_S are pairwise independent from γ and from α_T and α_S, respectively (Jost 2007; Baselga 2010). Using simulations, we demonstrate below that β_T and β_S are pairwise independent from each other and are both pairwise independent from α.

2. The values of β_S (resp. β_T) are intuitive and can be interpreted as 'the number of virtual, fully dissimilar and equally abundant site pools (resp. time pools)' in the study region.

3. The values of β_S, β_T and β have a range that is only dependent on the weights of, respectively, the site pools, time pools and the communities:

$$1 \le \beta_T \le N_T, \text{ with } N_T = \exp\left[-\sum_{t=1}^{T}\omega_t \times \log(\omega_t)\right]$$

$$1 \le \beta_S \le N_S, \text{ with } N_S = \exp\left[-\sum_{s=1}^{S}\omega_s \times \log(\omega_s)\right]$$

$$1 \le \beta \le N_{ST}, \text{ with } N_{ST} = \exp\left[-\sum_{t=1}^{T}\sum_{s=1}^{S}\omega_{st} \times \log(\omega_{st})\right]$$

The minimum possible value of β_S, β_T and β will be 1 if the site pools, time pools or communities, respectively, are identical. The maximum possible value of β_S, β_T and β will be attained if the site pools, time pools or communities, respectively, do not share species or tree branches. N_S, N_T and N_{ST} can be interpreted as the equivalent number of sites pools, times pools and communities, respectively. If all communities are weighted equally, they will be equal to S, T and ST, respectively.

In other words, our measurement of change in diversity over space (resp. over time) has a natural minimum and maximum. Thus the absolute values of β_S and β_T can be standardized by their minimum and maximum value to make their value independent from the number of sites and time periods studied (Chao, Chiu & Hsieh 2012): ${}^{\text{Std}}\beta_S = \frac{\beta_S - 1}{N_S - 1}$ and ${}^{\text{Std}}\beta_T = \frac{\beta_T - 1}{N_T - 1}$

β_{ST} has a minimum value of 1 and a maximum value constrained by both the value of β_S and β_T (see Appendix S2 for the demonstration),

$$1 \le \beta_{ST} \le \min\left(\frac{N_{ST}}{N_S} \times \frac{1}{\beta_T}, \frac{N_{ST}}{N_T} \times \frac{1}{\beta_S}\right).$$

RELATIONSHIP TO THE NESTED DECOMPOSITION OF DIVERSITY

Another methodological choice that can be made when analysing a spatio-temporal data set is to consider that space and time are nested (e.g. Sobek *et al.* 2009). If space is considered as nested within time periods, a new measure $\beta_{S/T}$ can be formulated to characterize the mean spatial β-diversity of the region within time periods (Pavoine & Dolédec 2005; Tuomisto 2010).

The decomposition will then be expressed as:

$$\gamma = \beta_T \times \beta_{S/T} \times \alpha \qquad \text{eqn 7}$$

meaning that

$$\beta_{S/T} = \frac{\alpha_T}{\alpha} = \beta_S \times \beta_{ST}$$

Alternatively, if we consider time periods as nested within space:

$$\gamma = \beta_S \times \beta_{T/S} \times \alpha \quad \text{eqn 8}$$

meaning that

$$\beta_{S/T} = \frac{\alpha_S}{\alpha} = \beta_T \times \beta_{ST}$$

.

Thus, $\beta_{S/T}$ and $\beta_{T/S}$ are not strictly β-diversities because they are the ratio of two mean α-diversities from different hierarchical levels, rather than the ratio of a unit's diversity and the diversity of its subunits. However, we demonstrated (Appendix S1) that like β-diversities, they have fixed minimum and maximum values that are independent of the γ- and α-diversities: $1 \leq \beta_{S/T} \leq \frac{N_{ST}}{N_T}$ and $1 \leq \beta_{T/S} \leq \frac{N_{ST}}{N_S}$.

INTERPRETATION OF β-DIVERSITIES

The different β-diversities can be interpreted on their own and in combination with each other (Fig. 1). β_T quantifies the change in diversity between time pools, or in other words, the temporal change in regional diversity, irrespective of the spatial patterns of diversity. β_S quantifies the change in diversity between site pools, or in other words, the spatial change in diversity after averaging the temporal variability of communities. β_{ST} quantifies the interaction between spatial and temporal turnover, it can be used to quantify finer changes such as a rearrangement of species between sites between two dates which are not quantified by β_S and β_T (Fig. 1). The case where β_{ST} is equal to 1 indicates that there is an identical change of diversity across space and time between communities, for instance, if between two dates a species is introduced in all studied communities at equal relative abundance. On the other hand, a value of β_{ST} over 1 denotes a heterogeneity of change of communities over space and time that is not quantified by β_S and β_T because it averages out at larger spatial or temporal scales. It is interesting to note that it is possible to have a situation where β_S and β_T equal one while β_{ST} is higher than one. This is illustrated in Fig. 1 ($\beta_S = \beta_T = 1$ and $\beta_{ST} > 1$) with an extreme case in which two communities fully inversed their composition between the two dates studied. A concrete example could be the mosaic theory of forest regeneration (Remmert 1991): disturbances in a forested landscape would trigger the same temporal successions but at different times and locations generating a heterogeneous landscape. In this case, there is a spatial and temporal change between communities, but the time pools remain constant (in other words, the diversity of the region changes very little between the two dates) and the site pools also remain constant (in other words, when averaged over time, communities across the landscape have a similar composition).

TEST OF FUNCTIONAL AND PHYLOGENETIC β-DIVERSITIES

A common way to test the values of functional or phylogenetic β-diversities is to use a randomization model to generate a distribution of β-diversities under a certain null hypothesis. Our framework is compatible with any kind of randomization procedure. In the following case study of French avifauna, we chose the species shuffling procedure that has been shown to be among the most efficient null models in terms of Type I error rate (Hardy 2008). A significant high (resp. low) β-diversity thus indicates that species tend to be replaced by dissimilar (resp. similar) species over time or space. We calculated the effect size of each functional β-diversity, as the observed β-diversity minus the mean of its null distribution divided by the standard deviation of the null distribution. If the β-diversity was higher than expected (positive effect size), then the communities differed more than expected under a random assembly model; if the β-diversity was lower than expected (negative effect size), then the communities differed less than expected under a random assembly model.

Independence properties of the spatio-temporal diversity decomposition

We adapted the simulation procedures developed by Baselga (2010) to demonstrate the independence properties of our diversity decomposition framework. We used two simulation approaches: (i) a top-down approach where we first chose a γ value, then generated a community weight vector and sequentially randomly selected the values of α_T, α_S and α; (ii) a bottom-up approach where we first chose an α value, then generated a community weight vector and sequentially randomly selected the values of α_T, α_S and γ. Each draw was constrained by minimum and maximal values deduced from the properties of the spatio-temporal decomposition stated above. For a given number of sites (S) and dates (T), we tested 200 initial γ or α values between 1 and 200, each repeated 200 times. Both the top-down and bottom-up approach procedures are detailed in Appendix S3. Both procedures are necessary to demonstrate the pairwise independence of the β-diversities from γ and α (Baselga 2010). In the top-down approach, the β-diversities need to be uncorrelated with γ, and in the bottom-up approach, the β-diversities need to be uncorrelated with α.

When no data were missing (i.e. all sites observed at all times) and $T = 4$ and $S = 10$, we found no correlation of γ with $^{Std}\beta_T$ (Fig. 2, $r = -0{\cdot}0014$; 95% CI interval: [−0·011, 0·0084]), γ with $^{Std}\beta_S$ (Fig. 2, $r = -0{\cdot}0013$; 95% CI interval: [−0·011, 0·0085]) or $^{Std}\beta_T$ with $^{Std}\beta_S$ (Fig. 2, $r = -0{\cdot}0019$; 95% CI interval: [−0·012, 0·008]) in the top-down approach and no correlation of α with $^{Std}\beta_T$ or α with $^{Std}\beta_S$ in the bottom-up approach (Fig. S1. α and $^{Std}\beta_T$: $r = 0{\cdot}0052$; 95% CI interval: [−0·0046, 0·015]). In contrast, β_{ST} depended on the previously established β_T and β_S values, but is independent from both γ and α (Fig. 2. β_{ST} and γ: $r = 0{\cdot}00038$; 95% CI interval: [−0·0094, 0·010] Fig. S1. β_{ST} and α: $r = 0{\cdot}0037$; 95% CI interval: [−0·0061, 0·0135]). When we further explored alternative T and S parameterizations (for any values of S and T between 2 and 10), we found these results to be robust (Table 1).

We also investigated the specific case where community data were missing in the data set. For all T and S parameter values, a varying proportion of community weights were set to 0 while

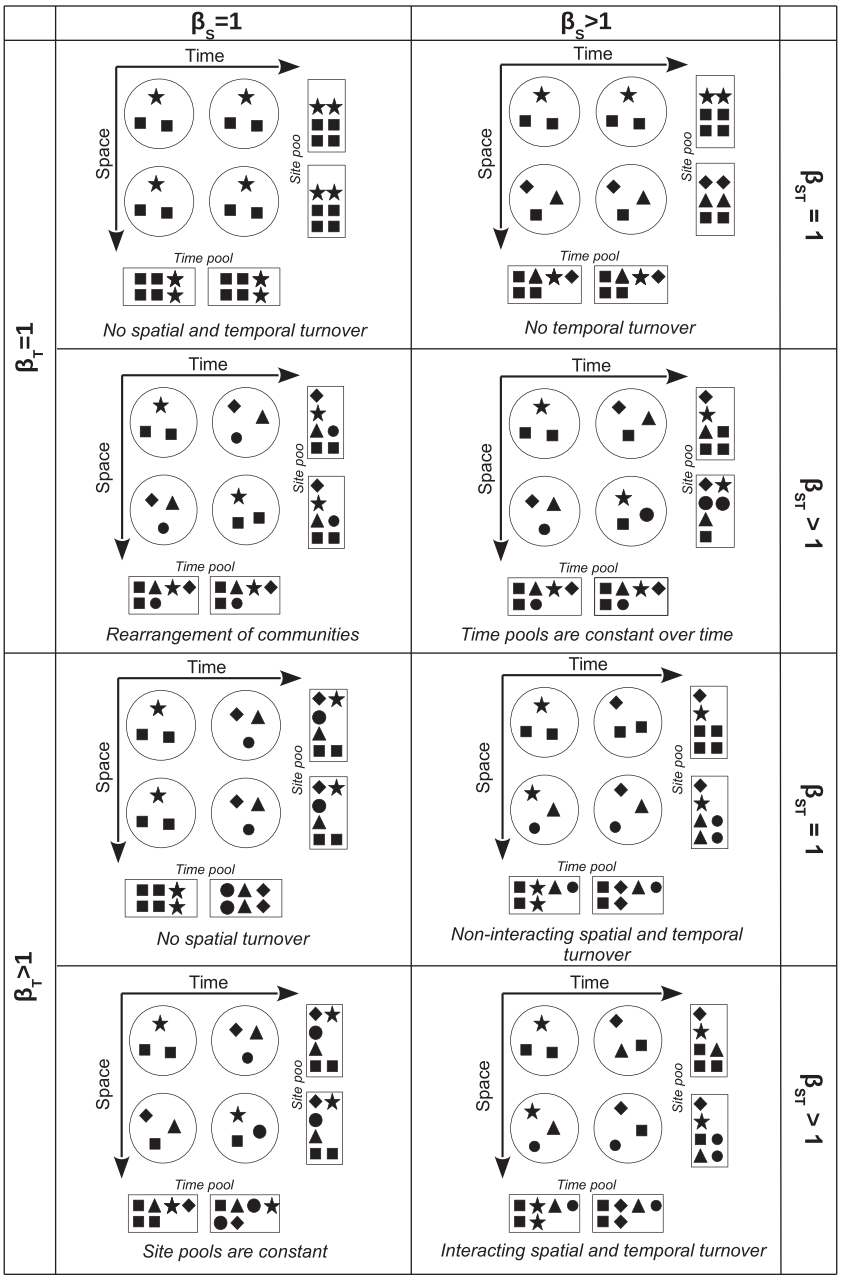

Fig. 1. Graphical interpretation of the eight possible patterns of diversity change over space and/or time and their respective β_S, β_T, β_{ST} value. Each cell of the table represents one of the patterns illustrated by the composition of four communities from two sites (lines) at two dates (column), each represented by a circle. Sites and time pools (see Methods) composed from the pooled composition of communities over sites or dates, respectively, are represented by rectangles. Within communities and pools, symbols represent individuals from a species specified by the geometrical shape.

maintaining at least one community per site and date. We then studied how the amount of missing data affects the independence properties between γ, β_T, β_S, β_{ST} and α. We found that in the extreme case of perfect balance (all community weights are equal), all correlations remained close to 0. When we introduced unequal weighting and increased the proportion of missing data, the correlation between β_T and β_S increased slightly but remained on average close to 0. However, there were some extreme correlation values that deviated strongly from 0. We observed the same pattern for the other relationships although they tended to show more robustness (Fig. 3). This can be explained by the fact that the sampling design becomes less orthogonal between sites and dates as the amount of missing data increases. The extreme case would be a spatial-temporal data set where a single community was sampled per date, each time at different sites. Then β_T and β_S would be equal. However, as indicated by the correlation values, which were on average close to 0, the independence relationship remained on average quite robust and only a few weight vectors resulted in a loss of the independence properties.

Overall, we therefore conclude that β_T, β_S and β_{ST} are pairwise independent from α and γ. We further conclude that β_T and β_S are pairwise independent from each other but only when the weighting scheme does not deviate too far from a perfectly balanced sampling design (i.e. no missing data and for all s and t, $\omega_{st} = \frac{1}{ST}$).

Our simulation procedure has its limitations. Indeed, it is not clear how the inclusion of a phylogenetic or functional tree between species could further constrain the distribution of the different diversity metrics compared to the maximal values of

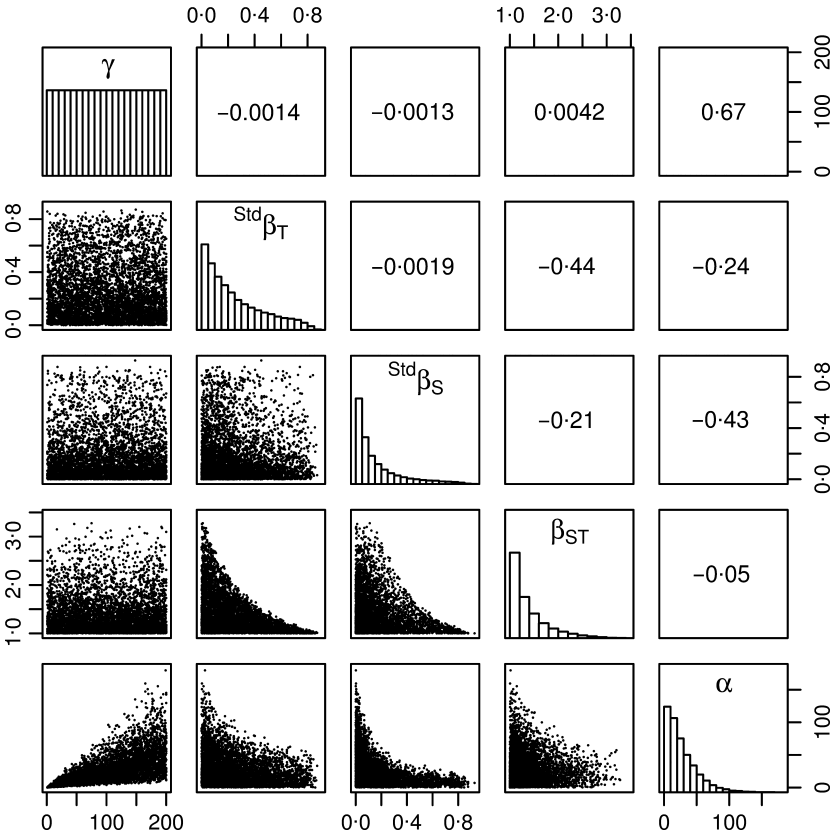

Fig. 2. Pairwise scatterplot of the value of γ, ${}^{Std}\beta_T$, ${}^{Std}\beta_S$, β_{ST} and α obtained from a 'top-down' simulation procedure. T was equal to 4 and S to 10. The panels on the diagonal represent the distribution of each diversity estimate over the simulations. The panels from the lower triangle represent the pairwise relationship between two of diversity estimates, and the panels from the upper triangle contain the Pearson correlation coefficient between two of diversity estimates.

β_T, β_S and β_{ST} previously fixed. It is, however, intuitive that the maximum number of completely distinct communities, site pools or time pools is equal to the number of functional/phylogenetic tree branches that emerge from the root. Therefore, although our simulation procedure concords with the current understanding of the diversity decomposition using Chao's index, it should be specified that our approach is more strictly appropriate for borderline cases where species are fully distinct or when the inclusion of a functional or phylogenetic tree does not affect the potential distribution of the diversity measures. In other cases, it is possible that the independence properties we empirically accessed would be altered.

Case study: spatio-temporal changes in functional diversity in French bird assemblages

DATA

We applied our spatio-temporal framework to the avifauna monitored by the French breeding bird survey programme (Julliard *et al.* 2006). This programme relied on skilled ornithologists to monitor common birds using a standardized protocol from 2001 to 2012. Under this scheme, ornithologists recorded every individual seen or heard during a five-minute period at 10 count points, evenly distributed within 2 × 2 km survey sites. The sites were randomly selected around the observer's locality, thus ensuring that a variety of habitats were monitored (including intensive farmlands, forests, suburbs and cities). We selected four regions, each defined as a circular window 100 km in diameter, belonging to two disparate biogeographical regions. Two were situated on the Mediterranean coast (MED1 and MED2) and two on the Atlantic coast (ATL1 and ATL2). Each region included different numbers of survey sites for which temporal trends were available (i.e. with sites monitored twice at least five years apart). 'Communities' were defined as the species assemblages recorded at the sites in the different regions. Species similarity was estimated from the ultrametric functional tree taken from Thuiller *et al.* (2014) based on body mass, diet and feeding behaviour (see Appendix S4 for details). Each community was given the same weight.

Table 1. Correlation coefficients between diversity measures according to the simulation procedure for a given T and S value. The table displays the range of coefficients over the tested values of T and S ($2 \leq T \leq 10$; $2 \leq S \leq 10$). Asterisks indicate correlation coefficient intervals close to 0

Diversity measures	Top-down approach	Bottom-up approach
γ and ${}^{Std}\beta_T$	[−0·0143, 0·0117]*	[0·149, 0·598]
γ and ${}^{Std}\beta_S$	[−0·0137, 0·0153]*	[0·146, 0·596]
γ and β_{ST}	[−0·0137, 0·0142]*	[−0·181, −0·0653]
γ and α	[0·485, 0·912]	[0·485, 0·915]
${}^{Std}\beta_T$ and ${}^{Std}\beta_S$	[−0·0137, 0·0270]*	[−0·107, 0·193]
${}^{Std}\beta_T$ and β_{ST}	[−0·559, −0·0725]	[−0·414, −0·185]
${}^{Std}\beta_T$ and α	[−0·486, −0·111]	[−0·0162, 0·0136]*
${}^{Std}\beta_S$ and β_{ST}	[−0·560, −0·0695]	[−0·415, −0·188]
${}^{Std}\beta_S$ and α	[−0·490, −0·106]	[−0·0145, 0·0124]*
β_{ST} and α	[−0·182, 0·0206]	[−0·0150, 0·0159]*

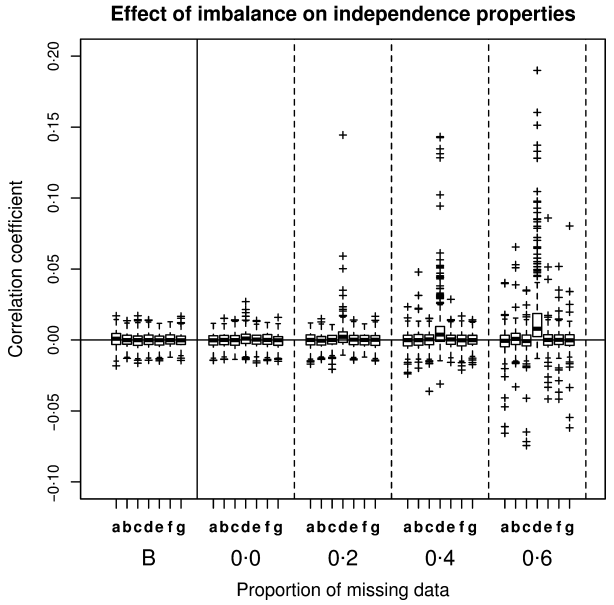

Fig. 3. Boxplots of the correlation coefficients obtained from the simulations as a function of the percentage of missing data (e.g. community weights set to 0). The boxplot on the far left (designated by 'B') illustrates the case of perfect balance (all community weights are equal). The figure displays the correlations between (a) γ and ${}^{\mathrm{Std}}\beta_T$ given by the top-down procedure, (b) γ and ${}^{\mathrm{Std}}\beta_S$ given by the top-down procedure, (c) γ and β_{ST} given by the top-down procedure, (d) ${}^{\mathrm{Std}}\beta_T$ and ${}^{\mathrm{Std}}\beta_S$ given by the top-down procedure (e) ${}^{\mathrm{Std}}\beta_T$ and α given by the bottom-up procedure, (f) ${}^{\mathrm{Std}}\beta_S$ and α given by the bottom-up procedure and (g) β_{ST} and α given by the bottom-up procedure.

Mathematically, this means that for all s and t, $\omega_{st} = \frac{1}{ST}$. To further facilitate the interpretation of the result of the spatio-temporal decomposition, we used a double principal component analysis (*dpcoa*, Pavoine, Dufour & Chessel 2004) to visualize the differences between the sites in each region in terms of functional composition (Appendix S5 and Fig. S2). A summary of the information on the four regions is available in Table 2.

Results

SPATIAL β-DIVERSITY

Absolute values of spatial β-diversities differed strongly between the four regions (Fig. 4). We found that MED2 > ATL2 > MED1 > ATL1 regarding spatial β-diversity. When focusing on standardized β-diversity, the ranking between regions changed: the spatial β-diversity of the region MED2 (which contained 14 sites) appeared much smaller such as ATL2 > MED1 > MED2 > ATL1. This was confirmed by the multivariate analysis, where MED2 appeared less spatially structured across the main multivariate axis compared to the other regions (Appendix S5, Fig. S2). The region MED1 and the region ATL2 stood out for their high values of standardized spatial β-diversity which indicated that the site pools were more distinct in these regions than in the other two regions. This difference could be due to greater region-wide environmental heterogeneity in MED1 and ALT2 compared to MED2 and ALT1. The null model made it possible to determine that the site pools of the region MED1 were more functionally different (albeit marginally) than expected from their taxonomic composition compared to ATL2 despite having a lower standardized value of spatial β-diversity (MED1, effect size of $\beta_S = 1{\cdot}22$; ATL2, effect size of $\beta_T = 0{\cdot}21$; Fig. 4). The multivariate analysis of MED1 (Fig. S2) further suggested that sites at both dates were differentiated mainly according to the body size of their constituent species, suggesting a degree of large-scale environmental filtering acting on the birds' functional traits. On the other hand, the difference between the ATL2 site pools was not significantly different from the random expectation. This suggests that the large functional difference between site pools was due to a large number of different species (hence the high spatial β-diversity) but that between the site pools, these species were not particularly distinct in terms of their functional traits.

TEMPORAL β-DIVERSITY

Overall, the temporal change in regional diversity was more substantial in the two Mediterranean regions than in the two Atlantic regions (Fig. 4). However, the use of the null model showed that the temporal β-diversity in MED1 was much higher than expected from the taxonomic change (effect size = 3·09) while in MED2, the temporal β-diversity was only marginally different from the taxonomic change (effect size = 1·48). This showed that between the two dates studied, the MED1 time pools were significantly different in terms of the functional traits of their constituent species (as suggested by the multivariate analysis, this was most likely due to the relative increase in larger-bodied species in all the sites over time, Fig. S2). In contrast, the two Atlantic regions showed low temporal β-diversity, and the null model further showed that it was even lower than expected from the taxonomic change for ATL1 (ATL1, effect size of $\beta_T = -1{\cdot}87$; ATL2, effect size of $\beta_T = 0{\cdot}15$; Fig. 4). This indicated that the sites studied in ATL1 remained remarkably constant over time, with species being substituted by other species with similar functional traits. Overall, these results are consistent with previous diachronic analyses, which demonstrated substantial changes in bird communities in inland Mediterranean areas over time due to major changes in land use (Preiss, Martin & Debussche 1997; Sirami, Brotons & Martin 2007).

INTERACTION TERM

The interaction term β_{ST} was always higher than 1 across the four regions studied. However, as the value of β_{ST} is dependent on both β_T and β_S and the study design (number of sites and number of dates), it was difficult to compare it across regions. The null model provides a way of determining whether the interaction term was higher or lower than expected from the taxonomic turnover. We found that the interaction term of β_{ST} was much higher than expected (effect size = 1·99) indicating that individual sites changed more in functional composition

Table 2. Characteristics of the different regions

Region	Biogeographical zone	Number of sites	First year	Final year	Size of the species pool	Functional γ-diversity	Functional α-diversity
MED1	Mediterranean	5	2003	2008	63	8·06	6·48
MED2	Mediterranean	14	2003	2009	57	10·75	7·22
ATL1	Atlantic	7	2003	2009	43	8·32	6·73
ATL2	Atlantic	5	2003	2009	44	8·69	6·10

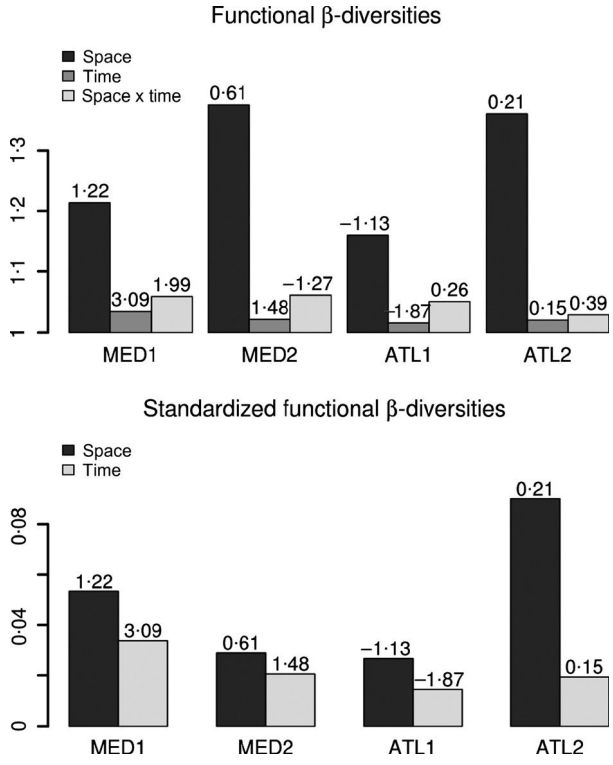

Fig. 4. Functional β-diversity decomposition between spatial (dark grey), temporal (grey) and spatial-temporal interaction (light grey) components for each of the four regions. Each bar represents the absolute value of the β-diversity (top) or its value standardized by its minimum and maximal possible value (bottom). Numbers above each bar show the effect size against the null model. A negative value indicates a higher than expected value of β-diversity while a positive value indicates a lower than expected value of β-diversity.

than expected from the temporal trend at regional level (β_T). Furthermore, the case of ATL1 is interesting because while β_S and β_T are both lower than expected, β_{ST} is marginally higher than expected (effect size = 0·26). We interpreted this as a case of a region with communities whose functional composition had changed markedly over time, but in opposite directions. This indicates potential for investigating β_{ST} as an emergent spatio-dynamic component of community changes.

Perspectives and limitations of spatio-temporal decomposition

The novel methodology presented herein has several advantages and strengths. Firstly, it allows a standardized decomposition of diversity across regions with potentially very different γ-diversities. In France, the functional and phylogenetic γ-diversities of avifauna are heterogeneous across space due to different macro-climatic influences (Devictor *et al.* 2010). Most notably, the Mediterranean Basin has high taxonomic, functional and phylogenetic γ-diversity, which contrasts with the rest of France. Using our methodology, β-diversities are found to be pairwise independent from the local γ-diversities, thus making it possible to study processes such as landscape heterogeneity or land use change across regions without interference from the biogeographical differences quantified by the γ-diversities. In contrast, there was a risk with the original *Anodiv* procedure (Rao 1986) of yielding overestimated values for β-diversities in biogeographical areas with high γ-diversities, regardless of the actual spatial or temporal change (Baselga 2010).

Secondly, our methodology accounts for differences in sampling efforts between regions. In our case study, spatial and temporal functional β-diversities were standardized using the maximum and minimum value they could possibly attain in a region (Fig. 4), thus producing estimates of β-diversities that were unrelated to the number of sites or dates studied within each region (Chao, Chiu & Hsieh 2012). Although our method does not prevent bias if the sampling is not representative of the biodiversity in a region over space and time, the standardization makes it possible to compensate for an unbalanced study design between regions. This solves a common problem arising from large-scale biodiversity monitoring where remote areas tend to be under sampled (Jiguet *et al.* 2012; Ficetola *et al.* 2013).

Thirdly, our approach also makes it possible to test the space-for-time substitution often used when time-series data are not available. The drivers of diversity change such as climate (e.g. Blois *et al.* 2013) or land use (e.g. Sirami, Brotons & Martin 2007) can be studied both across space and time. Ecologists have thus traditionally used space-for-time substitution as an alternative to expensive and rare long-term studies (Pickett 1989; e.g. Chalmandrier *et al.* 2013). This substitution assumes that changes in diversity over spatial locations and changes in diversity over time are equivalent and independent under the assumption that they are driven by the same ecological process (Fukami & Wardle 2005). However, this assumption can easily be violated by confounding processes such as dispersal (Brotons, Pons & Herrando 2005), biotic interactions (Thuiller *et al.* 2007) and delayed responses to changes in the local environment (Devictor *et al.* 2012). Our methodology provides tools which are adapted to testing the assumption on

which space-for-time substitution is based: the pairwise independence of β_S and β_T allows for the direct comparison of the spatial and temporal components of changes in diversity. However, we showed that this independence property was only maintained if the sampling design is balanced (i.e. there is relatively a low amount of missing data, and communities have a similar weight). We therefore recommend testing the sampling design beforehand using the simulation procedures to assess whether β_S and β_T are theoretically pairwise independent.

Fourthly, this is the first study to adapt the diversity decomposition between multiple factors originally proposed by Rao (1986) to the requirements of β-diversities computations, as recommended by Jost (2007) and Tuomisto (2010). Furthermore, we generalize this approach using Chao's index (2009) which includes species' functional and phylogenetic distances, thereby combining the advantages of both methods. Shannon entropy exponential and its generalization are the only equivalent numbers that fully combine the properties of the additive and multiplicative α-, β-, γ-decomposition (Jost 2007). This opens promising avenues for adapting our framework to methodologies based on the additive decomposition of the Shannon entropy (e.g. Pélissier & Couteron 2007). It is also the only equivalent number where (i) there is more or less a general consensus about the handling of unequal weighting of communities (but see Chiu, Jost & Chao 2014) and (ii) the unequal weighting still leads to β-diversities values that are pairwise independent from γ- and α-diversities (Jost 2007; Tuomisto 2010).

Chao's index belongs to a large family of indices that extend the Hill numbers (1973) to include species' phylogenetic similarities (Chao, Chiu & Jost 2010) making it possible to explicitly parameterize the weight given to a rare vs. a dominant species. While our framework is transposable to these indices, some properties (pairwise independence of β-diversities from γ- and α-diversities, range of β_{ST} and of nested β-diversities) need to be demonstrated, in particular in the case of missing data and unequal weighting of communities. The Chao's index studied is based on assumptions on how to take into account species abundances, that is the contribution of a species to the diversity value is proportional to its relative abundance (Chiu, Jost & Chao 2014). It thus may not be suitable for achieving certain analytical aims: for instance, a conservation approach may want to consider rare and dominant species equally regardless of their relative abundance. On the other hand, a focus on ecosystem functioning may require an emphasis on dominant species as they are expected to be the main contributors to ecosystem functioning (Garnier *et al.* 2004; but see Mouillot *et al.* 2013). Furthermore, recent work has shown the value of analysing diversity patterns with multiple equivalent numbers in order to vary the weighting given to dominant as opposed to rare species and to disentangle multiple assembly rules (Arroyo-Rodriguez *et al.* 2013; Chalmandrier *et al.* 2014b). We therefore argue for more statistical development to adapt spatio-temporal decomposition to other equivalent numbers, using the generalization of Hill numbers, and thus adding a supplementary parameter which explicitly examines the impact of species' relative abundances.

Conclusion

Recent years have seen major efforts to unify methodologies for evaluating and decomposing assemblage diversity. We have drawn on these achievements to propose a methodology that overcomes the challenges encountered when studying large-scale diversity data sets which encompass multiple orthogonal dimensions. We have shown that this approach can be used with classical animal survey data (also available for butterflies, fishes and plants) and that it provides clear results. Although more work is required to expand this method to multiple diversity indices, we believe that the properties of our methodology open up promising avenues for evaluating and testing diversity change across multiple dimensions. This will allow thorough analyses of the ever-increasing data produced by biodiversity survey programmes world-wide.

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Data accessibility

The site-by-species matrices and the functional tree of French avifauna are available online from the Dryad Digital Repository (Chalmandrier *et al.* 2014a).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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Fig. S1. Pairwise scatterplot of the value of γ, β_T, β_S β_{ST} and α obtained from a 'bottom-up' simulation procedure. T was equal to 4 and S to 10.

Fig. S2. Position of sites and species in the multivariate space defined by the *dpcoa*.

Appendix S1: Minimum and maximum value of nested β-diversities

For simplicity, space will be nested within time. The alternative (time nested in space) is also valid. (see Table S1 for notations)

We start from the formulation of the nested decomposition in a multiplicative framework (Pavoine *et al.* 2005, Tuomisto 2010) applied to the exponential of the Shannon entropy and its extension to phylogenetic and functional distances (Chao's index), we used a weighting scheme according to Jost 2007. Other weighting schemes have been proposed (Chiu et al. 2014) but only the weighting scheme of Jost produce estimates of β-diversity independent of α and whose range is comprised between 1 and the equivalent number of sites.

$$D(P..) = \frac{D(P..)}{exp[\sum_{t=1}^{T} \omega_t \times log(D(P.t))]} \times \frac{exp[\sum_{t=1}^{T} \omega_t \times log(D(P.t)]}{exp[\sum_{t=1}^{T}\sum_{s=1}^{S} \omega_{st} \times log(D(Pst))]} \times exp|\sum_{t=1}^{T}\sum_{s=1}^{S} \omega_{st} \times log(D(Pst))| \quad \text{(Equation 1)}$$

We can note this equation as: ${}^{q}\gamma = \frac{\gamma}{\alpha_T} \times \frac{\alpha_T}{\alpha} \times \alpha$ or $\gamma = \beta_T \times \beta_{S/T} \times \alpha$. As noted by Tuomisto (2010), $\beta_{S/T}$ is not strictly a β-diversity since it is the ratio of two mean α-diversities of nested hierarchical levels rather than the ratio of the γ-diversity of a unit and the mean α-diversities of its sub-units. In the following demonstration, we show that despite this, $\beta_{S/T}$ has the minimal and maximal value expected from a β-diversity.

Following Equation 1, $\beta_{S/T}$ can be expressed as:

$$\beta_{S/T} = \frac{exp[\sum_{t=1}^{T} \omega_t \times log(D(P_{.t}))]}{exp|\sum_{t=1}^{T}\sum_{s=1}^{S} \omega_{st} \times log(D(P_{st}))|} \quad \text{(Equation 2)}$$

Within each time period *t*, we can calculate the spatial β-diversity $\beta_{S/t}$ as:

$$\beta_{S/t} = \frac{D(P.t)}{exp[\sum_{s=1}^{S} \frac{\omega_{st}}{\omega_t} \times log(D(P_{st})]}$$. It is a β-diversity *per se*, for all *t*, $1 \leq \beta_{S/t} \leq N_{S/t}$, with

$$N_{S/t} = exp[-\sum_{s=1}^{S} \frac{\omega_{st}}{\omega_t} \times log(\frac{\omega_{st}}{\omega_t})]$$

We deduced:

$$log(D(P_{.t})) = log(\beta_{S/t}) + \frac{1}{\omega_t} \sum_{s=1}^{S} \omega_{st} \times log(D(P_{st}))$$

And then by substituting the previous equation into Equation 4:

$$\beta_{S/T} = \frac{exp|\sum_{t=1}^{T} \omega_t \times |log(\beta_{S/t}) + \frac{1}{\omega_t} \sum_{s=1}^{S} \omega_{st} \times log(D(P_{st}))||}{exp|\sum_{t=1}^{T} \sum_{s=1}^{S} \omega_{st} \times log(D(P_{st}))|}$$

$$\beta_{S/T} = \frac{exp[\sum_{t=1}^{T} \omega_t \times log(\beta_{S/t})] \times exp[\sum_{t=1}^{T} \sum_{s=1}^{S} \omega_{st} \times log(D(P_{st}))||}{exp[\sum_{t=1}^{T} \sum_{s=1}^{S} \omega_{st} \times log(D(P_{st}))]}$$

And then, $$\beta_{S/T} = exp[\sum_{t=1}^{T} \omega_t \times log(\beta_{S/t})]$$

We can here note, that $\beta_{S/T}$ is the geometric mean of within time periods β-diversity. We now use the minimal and maximal value of $\beta_{S/t}$ to characterize the range of $\beta_{S/T}$.

$$exp[\sum_{t=1}^{T} \omega_t \times log(1)] \leq \beta_{S/T} \leq exp[\sum_{t=1}^{T} \omega_t \times log(N_{S/t})]$$

$$1 \leq \beta_{S/T} \leq exp[-\sum_{t=1}^{T} \omega_t \times \sum_{s=1}^{S} \frac{\omega_{st}}{\omega_t} \times log(\frac{\omega_{st}}{\omega_t})]$$

$$1 \leq \beta_{S/T} \leq exp[-\sum_{t=1}^{T} \sum_{s=1}^{S} \omega_{st} \times [log(\omega_{st}) - log(\omega_t)])]$$

$$1 \leq \beta_{S/T} \leq \frac{exp[-\sum_{t=1}^{T} \sum_{s=1}^{S} \omega_{st} \times log(\omega_{st})]}{exp[-\sum_{t=1}^{T} \sum_{s=1}^{S} \omega_{st} \times log(\omega_t)]}$$

$$1 \leq \beta_{S/T} \leq \frac{exp[-\sum_{t-1}^{T}\sum_{s-1}^{S}\omega_{st} \times log(\omega_{st})]}{exp[-\sum_{t=1}^{T}\omega_{t} \times log(\omega_{t})]}$$

And finally, $1 \leq \beta_{S/T} \leq \frac{N_{ST}}{N_T}$

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Appendix S2: Minimal and maximal value of β_{ST}

Part 1 – β_{ST} is superior to 1

The minimum value that can take the interaction term β_{ST} in the Anodiv (Rao 1986) was explored by Burbea and Rao (1982). They established that the interaction term in the additive formulation of the Anodiv was always positive when using Shannon entropy. With the notations used in this study, this means that:

$$[\sum_{s=1}^{S}\omega_s \times H(Ps.)] + [\sum_{t=1}^{T}\omega_t \times H(P.t)] - H(P..) - \sum_{s=1}^{S}\sum_{t=1}^{T}H(Pst) \geq 0$$

with $$H(P) = -\sum_i p_i \times log(p_i)$$

Or in a multiplicative framework, $$\frac{exp[\sum_{s=1}^{S}\omega_s \times H(Ps.)] \times exp[\sum_{t=1}^{T}\omega_t \times H(P.t)]}{exp(H(P..)) \times exp[\sum_{s=1}^{S}\sum_{t=1}^{T}H(Pst)}] = \beta_{ST} \geq 1$$

This means that β_{ST} is always superior or equal to 1 when species are linked by a star-like tree. Such property was however, to our knowledge, not demonstrated for any ultrametric tree. But using the formulation of Chao's index established by Pavoine et al. (2011) and Chiu et al. (2014), we can however demonstrate that this is the case.

According to these authors, we can slice a phylogenetic tree into M intervals with each node defining an interval boundary. In each time interval k delimited by the nodes *k* and *k-1* of age t_k and t_{k-1}, we can look how species are grouped into taxa and calculate the Shannon entropy of the vector of relative abundance of the taxa ${}^kP$. The phylogenetic diversity is then calculated as:

$$D(P) = exp[\frac{1}{T}\sum_{k=1}^{M}(t_k - t_{k-1})H({}^kP)]$$

We can similarly decompose β_{ST} along these time intervals. According to the Equation 3 in the main manuscript:

$$\beta_{ST} = \frac{exp[\sum_{t=1}^{T}\omega_t \times log(D(P.t))] \times exp[\sum_{s=1}^{S}\omega_s \times log(D(Ps.))]}{D(P..) \times exp[\sum_{t=1}^{T}\sum_{s=1}^{S}\omega_{st} log(D(Pst))]}$$

By introducing Pavoine's formulation of the diversity index, we can thus deduce:

$$log(\beta_{ST}) = \sum_{t=1}^{T}\omega_t \times \frac{1}{T}\sum_{k=1}^{M}(t_k - t_{k-1})H(^kP.t) + \sum_{s=1}^{S}\omega_s \times \frac{1}{T}\sum_{k=1}^{M}(t_k - t_{k-1})H(^kPs.)] - \frac{1}{T}\sum_{k=1}^{M}(t_k - t_{k-1})H(^kP..) - \sum_{t=1}^{T}\sum_{s=1}^{S}\omega_{st}\frac{1}{T}\sum_{k=1}^{M}(t_k - t_{k-1})H(^kPst)$$

and

$$log(\beta_{ST}) = \frac{1}{T}\sum_{k=1}^{M}(t_k - t_{k-1}) \times [\sum_{t=1}^{T}\omega_t \times H(^kP.t) + \sum_{s=1}^{S}\omega_s \times H(^kPs.) - H(^kP..) - \sum_{t=1}^{T}\sum_{s=1}^{S}\omega_{st}H(^kPst)]$$

As stated before, we know that the sum within brackets is positive, we can conclude that β_{ST} is superior or equal to 1.

Part 2 – Range of β_{ST}

As exposed in the main text, β_{ST} can be expressed as a function of nested β-diversities:

$$\beta_T \times \beta_{ST} = \beta_{T/S} \text{ \& } \beta_S \times \beta_{ST} = \beta_{S/T}$$

These equations allow to characterize the minimum and maximum value that can take β_{ST}. We showed in Appendix 1 that:

$$1 \leq \beta_{T/S} \leq \frac{N_{ST}}{N_S} \text{ \& } 1 \leq \beta_{S/T} \leq \frac{N_{ST}}{N_T}$$

Then, $1 \leq \beta_T \times \beta_{ST} \leq \frac{N_{ST}}{N_S}$ & $1 \leq \beta_S \times \beta_{ST} \leq \frac{N_{ST}}{N_T}$

And, $\frac{1}{\beta_T} \leq \beta_{ST} \leq \frac{N_{ST}}{N_S} \times \frac{1}{\beta_T}$ & $\frac{1}{\beta_S} \leq \beta_{ST} \leq \frac{N_{ST}}{N_T} \times \frac{1}{\beta_S}$

By combining both inequalities and using the result of Part 1, we can conclude that:

$$max(1, \frac{1}{\beta_T}, \frac{1}{\beta_S}) \leq \beta_{ST} \leq min(\frac{N_{ST}}{N_S} \times \frac{1}{\beta_T}, \frac{N_{ST}}{N_T} \times \frac{1}{\beta_S})$$

As β_T and β_S are superior or equal to 1, we can conclude that:

$$1 \leq \beta_{ST} \leq min(\frac{N_{ST}}{N_S} \times \frac{1}{\beta_T}, \frac{N_{ST}}{N_T} \times \frac{1}{\beta_S})$$

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Appendix S3: Simulation procedures

I Summary of the spatio-temporal decomposition properties

Property 1: $1 \leq \beta_T \leq N_T$ and $1 \leq \beta_S \leq N_S$

Property 2: $1 \leq \beta_{ST} \leq min(\frac{N_{ST}}{N_S} \times \frac{1}{\beta_T}, \frac{N_{ST}}{N_T} \times \frac{1}{\beta_S})$

Property 3: $1 \leq \beta_{S/T} \leq \frac{N_{ST}}{N_T}$ and $1 \leq \beta_{T/S} \leq \frac{N_{ST}}{N_S}$

II "Top-down" simulation procedure

For given values of T and S, we fixed 200 evenly distributed values of γ between 1 and 200. For each value, we repeated the following procedure 100 times.

1) We generated a vector of community weights. The weight of each community was drawn in a gamma distribution (k = 2, $\theta = \frac{1}{2k \times ST}$). This set of parameters were chosen so that the mean of the weight probability distribution was 1/ST which correspond to the case were all communities are weighted equally. The vector of community weight was then divided by its sum to ensure that it sums to one. We then calculated N_{ST}, N_T, N_S.

2) We randomly fixed α_T. As stated by Property 1, $1 \leq \beta_T = \frac{\gamma}{\alpha_T} \leq N_T$, thus $\frac{\gamma}{N_T} \leq \alpha_T \leq \gamma$. Furthermore, by multiplying the left and right side of the inequality given by Property 2 by γ, we can deduce that:

$\gamma \leq min(\frac{N_{ST}}{N_S} \times \alpha_T, \frac{N_{ST}}{N_T} \times \alpha_S)$. And thus that $\gamma \frac{N_S}{N_{ST}} \leq \alpha_T$. We can conclude that:

$max(\frac{\gamma}{N_T}, \frac{N_S}{N_{ST}}\gamma) \leq \alpha_T \leq \gamma$

So we randomly drew α_T according to a uniform law set between these values.

3) We randomly fixed α_S. As stated by Property 1, $1 \leq \beta_S = \frac{\gamma}{\alpha_S} \leq N_S$, thus $\frac{\gamma}{N_S} \leq \alpha_S \leq \gamma$. Furthermore, by multiplying the left and right side of the inequality given by Property 2 by γ, we

can deduce that:

$\gamma \leq min(\frac{N_{ST}}{N_S} \times \alpha_T, \frac{N_{ST}}{N_T} \times \alpha_S)$.

This inequality implies that $\gamma \frac{N_T}{N_{ST}} \leq \alpha_S$. We concluded that $max(\frac{\gamma}{N_S}, \gamma \frac{N_T}{N_{ST}}) \leq \alpha_S \leq \gamma$.

So we randomly drew α_S according to a uniform law set between these values.

3) We randomly fixed α. As stated by Property 3, $1 \leq \beta_{S/T} = \frac{\alpha_T}{\alpha} \leq \frac{N_{ST}}{N_T}$ thus

$\alpha_T \times \frac{N_T}{N_{ST}} \leq \alpha \leq \alpha_T$. As stated by Property 3, $1 \leq \beta_{T/S} = \frac{\alpha_S}{\alpha} \leq \frac{N_{ST}}{N_S}$, thus

$\alpha_S \times \frac{N_S}{N_{ST}} \leq \alpha \leq \alpha_S$. Furthermore, should the spatio-temporal structure of the dataset be ignored, we can state that, $1 \leq \beta_T \times \beta_S \times \beta_{ST} = \frac{\gamma}{\alpha} \leq N_{ST}$. Thus, $\frac{\gamma}{N_{ST}} \leq \alpha \leq \gamma$. And finally, as stated by Property 2, $\beta_{ST} = \frac{\alpha_T \times \alpha_S}{\gamma \times \alpha} \geq 1$, we can deduce that $\alpha \leq \frac{\alpha_T \times \alpha_S}{\gamma}$

In conclusion, we can characterize α as:

$max(\alpha_T \frac{N_T}{N_{ST}}, \alpha_S \frac{N_S}{N_{ST}}, \frac{\gamma}{N_{ST}}) \leq \alpha \leq min(\gamma, \alpha_T, \alpha_S, \frac{\alpha_T \times \alpha_S}{\gamma})$. So we randomly drew α according to a uniform law set between these values.

III Bottom-up procedure

For given values of T and S, we fixed 200 evenly distributed values of α between 1 and 200. For each value, we repeated the following procedure 100 times.

1) We generated a vector of community weights. The weight of each community was drawn in a gamma distribution (k = 2, $\theta = \frac{1}{2k \times ST}$). This set of parameters were chosen so that the mean of the weight probability distribution was 1/ST which correspond to the case were all communities are weighted equally. The vector of community weight was then divided by its sum to ensure that it sums to one. We then calculated N_{ST}, N_T, N_S.

2) We randomly fixed α_T. As stated by Property 3, $1 \leq \beta_{S/T} = \frac{\alpha_T}{\alpha} \leq \frac{N_{ST}}{N_T}$, thus $\alpha \leq \alpha_T \leq \frac{N_{ST}}{N_T}\alpha$.

So we randomly drew α_T according to a uniform law set between these values.

3) We randomly fixed α_S. As stated by Property 3, $1 \leq \beta_{T/S} = \frac{\alpha_S}{\alpha} \leq \frac{N_{ST}}{N_S}$, thus

$\alpha \leq \alpha_S \leq \frac{N_{ST}}{N_S}\alpha$.

So we randomly drew α_T according to a uniform law set between these values.

3) We randomly fixed γ. As stated by Property 1, $1 \leq \beta_T = \frac{\gamma}{\alpha_T} \leq N_T$, $1 \leq \beta_S = \frac{\gamma}{\alpha_S} \leq N_S$ and $1 \leq \beta = \frac{\gamma}{\alpha} \leq N_{ST}$. Furthermore, by multiplying the inequality given by Property 2 by γ, we can deduce that: $\gamma \leq \frac{\alpha_S \times \alpha_T}{\alpha}$. In conclusion, $max(\alpha_T, \alpha_S, \alpha) \leq \gamma \leq min(N_T\alpha_T, N_S\alpha_S, N_{ST}\alpha, \frac{\alpha_S\alpha_T}{\alpha})$. So we randomly drew γ according to a uniform law set between these values.

Appendix S4: Details of the construction of the bird functional tree

Trait data for the bird species in each region were extracted from the handbooks of the birds of the Western Palaearctic (BWPi 2006). Missing species and data were gathered from species publications and avifauna Internet websites (e.g. BirdLife). Traits were: Body mass, diet (invertebrates, vertebrates, vegetal, fish, carrion) and feeding behaviour (Pursuit (air and/or aquatic), sally, foliage/gleaning, pouncing, grazing, picking/pecking/stabing, digging, overturning, probing). For both diet and feeding behaviour, each sub-category was expressed as a binary state variable (0 or 1) to make sure a species could have several diet or feeding behaviour strategies (see Thuiller et al. 2014 for more details).

Body mass was log-transformed and normalized prior all analyses. We used a mixed-variables coefficient distance that generalized Gower's coefficient of distance to allow for the treatment of various types of variables when calculating distances (Pavoine *et al.* 2009). Euclidean distance was used for body mass, while the Sørensen distance was used for binary data type, as e.g. for each sub-group diet and feeding behaviour trait. We built a functional dendrogram linking all species in a functional space (UPGMA) to estimate ultrametric functional distances between species.

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Appendix S5: Comments on the multivariate analysis of the spatio-temporal changes of bird functional assemblages

The analysis sets the studied communities in the multivariate space according to the functional similarity between their constituent species. We used this approach to identify the functional groups that tended to vary across space and time to facilitate the interpretation of the spatio-temporal diversity decomposition. The *dpcoa* is based on Rao's quadratic entropy that does not strictly our diversity decomposition framework. It is however the only multivariate analysis, to our knowledge, that allows separating communities based on species distances.

The region MED1 presented a clear and opposite pattern with sites distinct over the first two multivariate axis, regardless of the date (Figure S2). Overtime, all five sites tended to shift towards higher scores along the first and second axis indicating that the assemblages became richer in bigger-bodied species. The region ATL2 also presented sites whose functional composition remained distinct overtime (Figure S4). The spatial turnover seemed to be mainly driven by the contrast between sites rich in between small bodied, insectivorous or vegetarian species and sites rich in the species from the other functional groups. Furthermore, ATL2 was remarkable because the functional composition of sites (apart from the two sites presenting a high proportion of small-bodied insectivorous species) changed little overtime. In contrast, ATL1 and MED2 did not exhibit clear spatial or temporal pattern. Sites seemed to changed little overtime (MED2) or seemed to exchange their composition (ATL1) and were overall quite similar between each other. (Figure S4).

Table S1: Notations for Appendix S1 and Appendix S2

Notation	Meaning	Formula or Property
	vector of the relative abundances of species *i* in the site *s* at the date *t*.	$\sum_{i=1}^{N} p_{ist} = 1$
ω_{st}	weight of the site *s* at the time period *t*	$\sum_{t=1}^{T}\sum_{s=1}^{S} \omega_{st} = 1$
ω_t	weight of the time period *t*	$\omega_t = \sum_{s=1}^{S} \omega_{st}$
ω_s	weight of the site s	$\omega_s = \sum_{t=1}^{T} \omega_{st}$
$P.t = \{p_{it}\}$	vector of species {i} relative abundances of the region at the time period *t*	$p_{it} = \frac{1}{\omega_t}\sum_{s=1}^{S} \omega_{st} p_{ist}$
$Ps. = \{p_{is}\}$	vector of species {i} relative abundances of the site across time periods	$p_{is} = \frac{1}{\omega_s}\sum_{t=1}^{T} \omega_{st} p_{ist}$
	vector of species {I} relative abundances over space and time in the region	$p_i = \sum_{t=1}^{T}\sum_{s=1}^{S} \omega_{st} p_{ist}$
N_{ST}	Equivalent number of communities	$N_{ST} = exp[-\sum_{t=1}^{T}\sum_{s=1}^{S} \omega_{st} \times log(\omega_{st})]$
${}^{q}N_S$	Equivalent number of site pools	$N_S = exp[-\sum_{s=1}^{S} \omega_s \times log(\omega_s)]$
${}^{q}N_T$	Equivalent number of time pools	$N_T = exp[-\sum_{t=1}^{T} \omega_t \times log(\omega_t)]$
D	Chao's index	
γ	Gamma diversity of the region	$D(P..)$
α_T	Mean alpha diversity of the time pools	$\alpha_T = exp[\sum_{t=1}^{T} \omega_t \times log(D(P.t))]$
α_S	Mean alpha diversity of the site pools	$\alpha_S = exp[\sum_{s=1}^{S} \omega_s \times log(D(Ps.))]$

α	Mean alpha diversity of the communities	$\alpha = exp[\sum_{t=1}^{T}\sum_{s=1}^{S}\omega_{st} \times log(D(Pst))]$
β_T	Temporal beta-diversity of the region controlled by the q parameter	$\beta_T = \frac{\gamma}{\alpha_T}$
$\beta_{S\setminus T}$	Spatial “beta-diversity” nested within time	$\beta_{S/T} = \frac{\alpha_T}{\alpha}$
$\beta_{S/t}$	Spatial beta-diversity within the time period t	

Figure S1. Pairwise scatterplot of the value of γï, β_T, β_S, β_{ST} and α obtained from a "top-down" simulation procedure. N_T was equal to 10 and N_S to 10. The panels on the diagonal represent the distribution of each diversity estimate over the simulations. The panels from the lower triangle represent the pairwise relationship between two of diversity estimates and the panels from the upper triangle contain the Pearson correlation coefficient between two of diversity estimates.

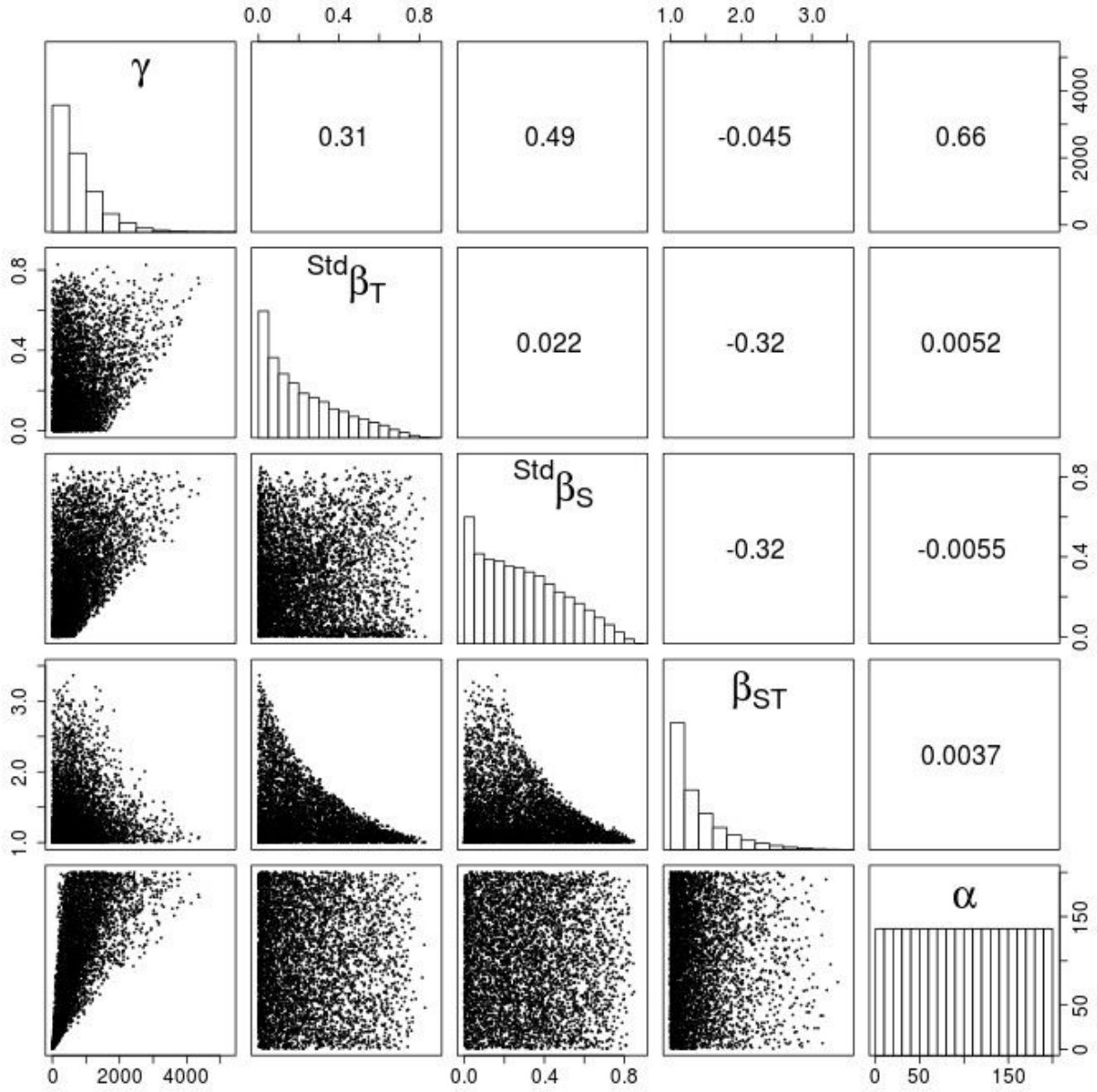
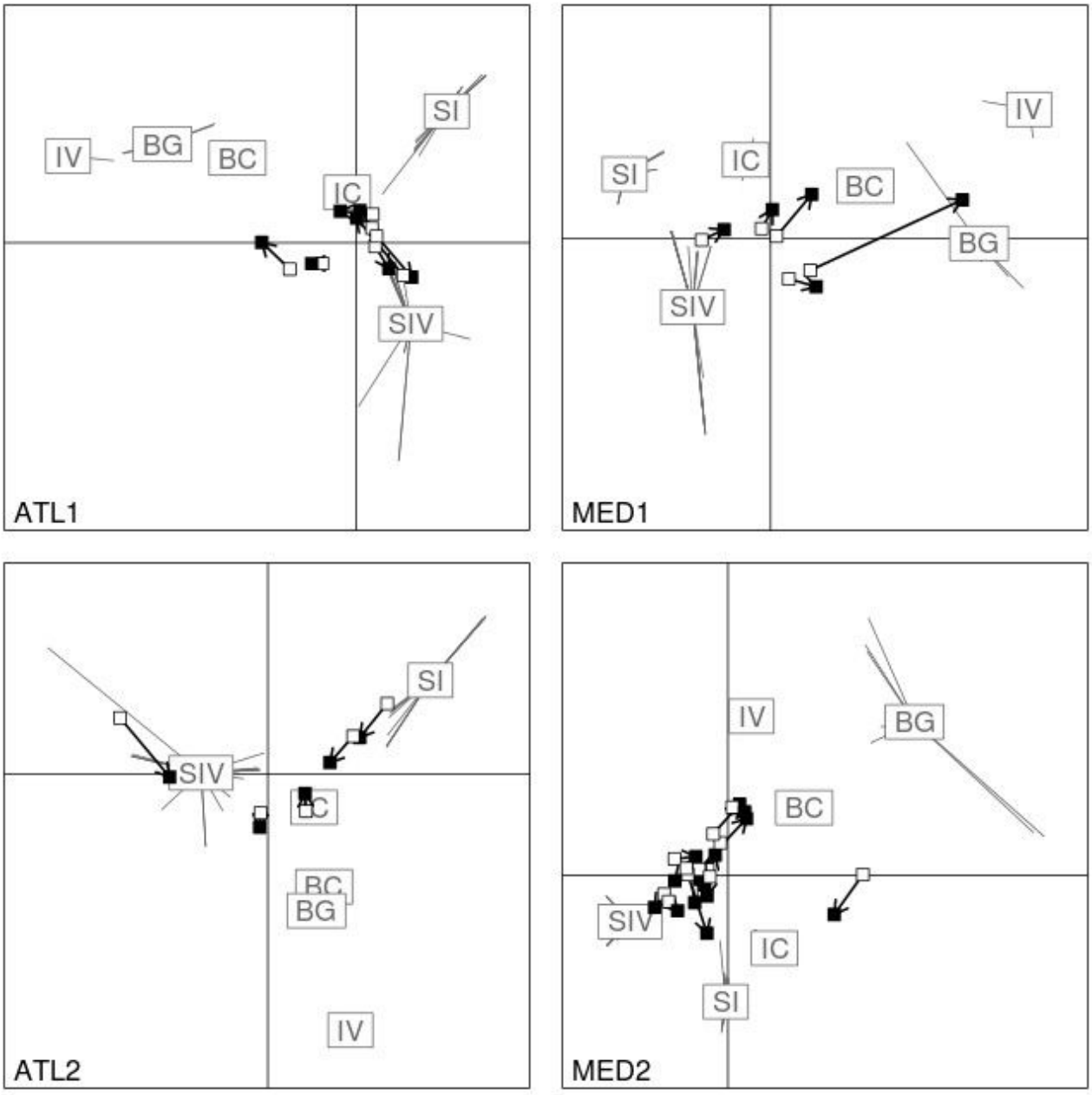


Figure S2 - Position of sites and species in the multivariate space defined by the *dpcoa* of the functional structure of bird assemblages in the four studied regions. White and black squares represent the site at the former and latter sampling dates, respectively. Arrows connect the same site at the two different dates. The stars connects together bird species of a given functional group obtained by cutting the functional tree into six of them. Abbreviations for functional groups are the following: BC - Big species with a carnivorous (i.e. eating vertebrates) diet; BG - Big species with various diets; SC - small carnivorous species; SI - Small insectivorous species; SIV - Small insectivorous and vegetarian species; SV - Small species with a vegetarian diet.



Troisième partie

Aspects méthodologiques de l'analyse des données de métabarcoding

Chapitre 5

Unravelling the invisible and quantifying the numerous : the promise of metabarcoding data for studying soil biotia diversity

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1 Introduction

The last few years have seen incredible developments in metagenomics (analysis of cellular microbial DNA) and in DNA barcoding (use of small DNA fragments that serve to discriminate among species, Valentini et al. [2009]). These developments have proved to be very important to understand the spatial and temporal variation of microbial communities. Indeed, while macro-organisms are relatively easy to follow through space and time in most places, soil biota that sustain important ecosystem functions and services are more difficult to quantify comprehensively through space and time. Environmental DNA metabarcoding (eDNA, Taberlet et al. [2012]) that now allows to get information about all extra-cellular DNA on a given soil sample have thus revolutionized microbial ecology [Green et al., 2008], and give incredible opportunities to analyze jointly all organisms that could be retrieved from soil samples (e.g. micro and macro organisms). Indeed, instead of having one given component of soil (e.g. fungi), we can now get access to bacteria, fungi, plants and other types of vertebrates depending on the available markers. This mass of data has the potential to be analyzed within the frameworks developed in both meta-community ecology on the joint analyses of taxonomic, functional and phylogenetic diversity patterns [Nemergut et al., 2013; Poisot et al., 2013], and in network theory on the variety of ecological interactions (e.g. mutualism, saprophytism, parasitism, predation...) through space and time [Morlon et al., 2014].

Measuring community diversity from eDNA is challenging. Compared to more traditional community studies, it is not species that define diversity but clusters of highly similar sequences that are called molecular taxonomic units (MOTU, Schloss and Handelsman [2005]). The main obstacle to the estimation of diversity is the typical long tail of rare MOTUs within and across samples which cast doubt on the reliability of diversity estimates [Bent and Forney, 2008; Haegeman et al., 2013].

Recent statistical developments have shown that among the plethora of existing diversity metrics [Pavoine and Bonsall, 2011], Hill numbers [Hill, 1973] can be a valuable tool for microbial ecology [Haegeman et al., 2013]. Hill numbers are a family of indices that generalized common diversity metrics such as richness, Shannon entropy and Simpson inverse into a single formula that depends of a parameter q. They have several qualities that makes them stand out from other diversity indices : (1) q is a sensitivity parameter that explicitly control the importance given to abundant MOTUs compared to rare ones ; (2) confidence intervals can be estimated [Chao et al., 2009; Haegeman et al., 2013] ; (3) diversity decomposition across space produce standardized estimates of β-diversity (community change across space) that can be easily interpreted [Jost, 2007] and whose value is not biased by the high values of microbial diversity [Bent and Forney, 2008] ; (4) finally Hill numbers have been recently extended to include phylogenetic relationships between MOTUs [Chao et al., 2010].

Although very promising, working with eDNA data is not as easy as working with

plant field samples. Indeed, the nature of eDNA data raises multiple methodological and conceptual challenges to the study of diversity patterns. These challenges mostly arise from the different steps between the sampling and the constitution of the dataset [Valentini et al., 2009].

Step 1. Not much is known about the sampling effort (i.e. the number of soil cores to sample) needed in a given location to obtain a representative sample of the local community diversity (α-diversity) as well of the diversity turnover across gradients (β-diversity). This is even more true when one focuses on microbial diversity that contain a high number of easily missed rare specimens and have quite likely faster distance decay than macroorganisms at a local scale [Astorga et al., 2012].

Step 2. The sampling, extraction and manipulation of eDNA samples inevitably lead to contaminations across samples or from the environment. These contaminations generate false background sequence diversity in the samples that can then lead to misleading diversity patterns or spurious homogeneity between samples. Furthermore the PCR amplification and sequencing can produce errors, with two important consequences for ecological analyses. First, those errors hamper to get reliable estimates of diversity from PCR-based data. Second, they limit the detection of rare species that become difficult to differentiate from noise [Cline et al., 1996]. Dealing with these technical issues is an ongoing challenge but there have been constant progresses in sequencing technology, bioinformatics tools and analytical pipelines [Bik et al., 2012].

Step 3. Only very short fragments can be amplified when working with degraded extracellular DNA found in soils. The taxonomic resolution of such short fragments is relatively low [Taberlet et al., 2007] and is limited for providing identification at the species level. Furthermore, eDNA metabarcoding requires high-quality taxonomic reference databases containing the targeted sequences of studied species. These reference datasets are constantly growing but are still largely partial, especially for microbial lineages. Consequently, for some sequences we do not know where exactly the MOTUs are supposed to be in the reference phylogeny, which lead also to uncertain phylogenetic diversity estimates.

Step 4. The diversity index choice may prove critical. Rare MOTUs are likely to be missed with low sampling effort or to be discarded during the filtering procedures of the second stage. As such indices that do not take into account MOTU abundance within samples are likely to be less robust than their abundance-weighted counterparts [Bent and Forney, 2008; Haegeman et al., 2013].

In this work, we examined empirically the first (sampling effort), third (taxonomic uncertainties) and fourth (diversity indices) steps and evaluate the impact of these sources of biases on diversity estimation. To do so, we studied twenty subalpine and alpine plots along a steep elevation gradient. Within each community, we sampled a maximum of twenty one soil cores, extracted eDNA and amplified it with five primer pairs to target the following lineages : Eucaryota, Viridiplantae, Fungi, Archea and Bacteria.

For each lineage, we estimated MOTU α-diversity in each community and β-diversity

across the gradient for varying sampling sizes (number of samples per 10 by 10m square plot) to test for the impact of biases linked to **Step 1**. α-diversities and β-diversity were estimated with different diversity indices from the Hill numbers family to test for the impact of the biases linked to **Step 4**.

In a second step, we studied the phylogenetic diversity of two of these lineages : Fungi and Viridiplantae for which phylogenies were available. To test the impact of taxonomic uncertainty (**Step 3**), we tested the robustness of Fungi and Viridiplantae phylogenetic α-diversities rankings to taxonomic uncertainties. Phylogenetic diversity indices were computed using backbone phylogenies in which MOTUs were placed according to their assignation. Two differents diversity indices were used to test for the impact of metric choices (**Step 4**).

We formulated the following hypotheses :

1. Sufficient sampling size will be lower when diversity is estimated from Hill numbers that take into account MOTUs abundance.
2. Sufficient sampling size to estimate β-diversity and α-diversity will increase with underlying sample heterogeneity within communities. Thus sufficient sampling size will differ between lineages : microbial lineages (Archea, Bacteria, Fungi) may require a higher sampling size because of high local turnover than macrobial lineages (Viridiplantae, some Eucaryota lineages).
3. β-diversity will require less sampling effort than α-diversity as large scale diversity turnover will be strong enough to counteract sample heterogeneity within communities.
4. Taxonomic uncertainty will affect the ranking of community phylogenetic diversity. Phylogenetic Hill numbers are likely to be as sensitive as their taxonomic counterpart to rare MOTUs. Given that, the taxonomic uncertainty of the large number of rare MOTUs is likely to make a phylogenetic richness metric such as Faith's index [Faith, 1992] will return less consistent results than an abundance-weighted metric such as Rao's quadratic entropy [Rao, 1986] which depends on a smaller number of abundant MOTUs. Furthermore, because the fungi phylogeny is less resolved than the plant phylogeny, fungi community phylogenetic diversity rankings will be less robust.

2 Methods

2.1 Study site & sampling

The study was conducted in the central French Alps (45.12°N, 6.40°E). (Figure 5.1). 10 sites were studied along a continuous 975 m elevation gradient (1750 - 2725 m) in a cow-grazed pasture. Subalpine grasslands dominated at the bottom of the gradient and alpine meadows with sparse vegetation at high elevation (Figure 5.1).

The ten sites were all on the same south-facing slope. In each site, we set up two square plots of 10 by 10 m separated by few meters. In each plot, 21 soil samples were collected along two transects that followed vegetation transects from another study [**?**]. The position of samples along these transects was optimized to have a uniform distribution of between-sample spatial distances (Figure 5.1,c). In total we collected 420 soil samples.

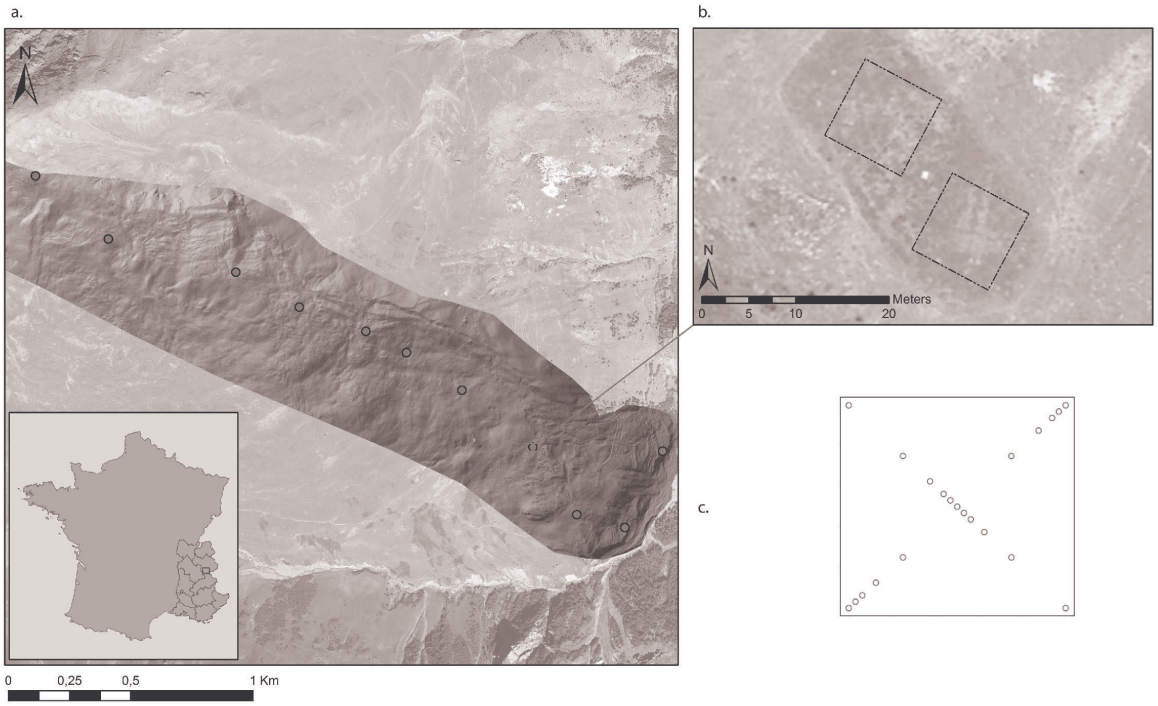

FIGURE 5.1 – Overview of the whole study area. a) Landscape scale, the dots indicates the position of the sites. b) Site containing the two 10 by 10m plots. c) Within plots, circles indicate the position where soil was sampled.

2.2 DNA extraction, amplification and sequencing

DNA extractions were carried out within 8h of sample collection to prevent DNA degradation and microbial growth in soil cores, as samples cannot be stored in proper condition at remote sites. Each soil core was broken up manually and then homogenized. Afterwards, 15g of soil were mixed with 15 ml of saturated phosphate buffer (Na_2HPO_4 ; 0.12 M ; pH 8), and shacked gently for 15 min (45 rpm). One ml of the resulting sludge was centrifuged at 11,000 g for 10 min. The supernatant was used as starting material for the NucleoSpin® Soil kit (Macherey-Nagel, Düren, Germany) according to the manufacturerâs instructions. In addition, a mixture of 16 plant species extracts with known concentration were used to constitute 48 positive controls at six different dilution factors (1, 2, 4, 8, 16, 32). The chosen plant species were spread across various plant lineages and had known reference sequences in Genbank in order to MOTU identification in positive controls to be straightforward. 20 extraction controls and 24 PCR controls were performed. Each sample was broken down into four replicates.

A set of five primer pairs were used for DNA amplification (Table 5.1). Three covered each one of the three domains of life (Archaea (*16s v8-9*), Bacteria (*16s v5-6*) or Eukaryota (*18s v7*)), while the remaining two covered particular Eukaryota subclades, (Fungi (primer *ITS1*) and Viridiplantae (primer *trnL* P6 loop)). The five selected markers were fully sequenced on Illumina HiSeq or MiSeq platforms. To discriminate samples after sequencing, both forward and reverse primers were tagged with a combination of two different 8-nucleotide long labels (hereafter designated as âtagâ). PCRs were carried out in a final volume of 30 µl, and contained 2 µl of DNA extract (including the negative controls), 1 U of AmpliTaq Gold® DNA polymerase (Applied Biosystems), 10 mM Tris-HCl, 50 mM KCl, 2 mM $MgCl_2$, 0.2 mM of each dNTP, 0.25 µM of each primer and 4.8 µl of bovine serum albumin (BSA, Roche Diagnostic). All PCR products were then purified (MinElute™ PCR purification kit, Qiagen), mixed together, and sequenced (Fasteris SA, Geneva, Switzerland). Libraries were loaded on Illumina HiSeq 2000 or MiSeq platforms depending on the marker length, and sequenced using the paired-end sequencing technology.

2.3 Data processing

Our aim was to minimize the occurrence of spurious MOTUs produced by PCR and sequencing errors. To that, we used two successive pipelines. The first one was devised by Zinger et al. [2015] and will not be detailed here. In summary, this pipeline sequentially performed the following steps : pair-end assembly, read assignment to samples, low quality reads removal, read dereplication, singleton removal, chimera detection and sequence clustering (i.e. MOTUs building). Taxonomic assignment of MOTUs was based on global alignment algorithm and full-length references gathered from the Genbank database. Whenever possible, we improved taxonomic assignments with more reliable taxonomic information [Koljalg et al., 2013; Pruesse et al., 2007; Willerslev et al., 2014]. When a given MOTU get more than one assignment, we prioritized assignment from the databases with the most reliable taxonomic information. This pipeline further accomplished additional and novel filtering steps to minimize the effect of sample cross contaminations that are also detailled in Zinger et al. [2015]. As the result of this pipeline, we finally obtained five sample-by-MOTUs matrices.

The Virdiplantae table was further filtered by a second pipeline that uses the positive controls of the *tnrL* marker as a calibration dataset to model the probability of remaining sequences to be errors or samples contaminants based on their abundance within samples and frequency across sample replicates. This pipeline is detailed in the supplementary material.

2.4 Estimating relative abundances

There is no consensus on how to measure the relative abundance of a MOTU in a sample from its number of sequences. To determine the best option, we compared the

Lineage	Number of MOTUs	Number of MOTUs per sample mean [min, max]	Sequences per sample	Minimum number of samples per plot
Archea	527	26.04 [6, 53]	1760	15
Bacteria	24038	2271 [381, 4019]	1629	19
Eucaryota	5833	830.31 [173, 1149]	51069	19
Viridiplantae	201	16.38 [8,22]	18217	21
Fungi	2956	172.98 [24, 306]	2468	19

TABLEAU 5.1 – Overview of the sample-by-MOTUs tables according to the considered lineage. The number of sequence per sample refers to the number of sequences after rarefaction.

performance of two metrics by using the positive controls. After having identified the species associated to each of the MOTUs detected in the positive controls, we tested which one of the two metrics correlated best with the initial concentration of plant extracts in the positive controls.

The first metric is based on the summed number of reads across sample replicates, $\frac{\bar{N_{ij}}}{\sum_i \bar{N_{ij}}}$. The second metric is the relative log-number of reads in the sample $\frac{log(\bar{N_{ij}}+1)}{\sum_i log(\bar{N_{ij}}+1)}$, with $\bar{N}_{ij}$ being the summed number of sequences of MOTU i in sample j across replicates. For each of the two metrics, we then estimate in each sample j, the Pearson correlation of the metric to the initial concentration of the different plant species extract in the positive controls. We found that the relative log-number of reads was performing best (mean correlation of 0.68 against a correlation of 0.58). It is therefore used for the rest of the analyses.

2.5 Estimating MOTU α and β-diversities as a function of sampling effort (S) and abundance weights (q)

Estimation of MOTU relative abundances

Based on the sample-by-MOTUs matrix, for each sample, we summed reads across replicates. To ensure that each sample had the same sequencing depth, we rarefied the matrix to the minimum number of reads found across sample (see Table 5.1). We then constructed the relative abundance matrix by randomly selecting S samples per plot and using the relative log-number of reads in the sample as our metric of MOTUs relative abundance.

Hierarchical decomposition of MOTUs diversity

We used the Hill numbers [Hill, 1973] to calculate MOTUs diversity across four hierarchial levels. These units were the landscape (pooled samples across the study sites), the site (pooled samples within sites), the community (pooled samples within plots) and the sample (see Figure 5.1).

We defined the vector P = p_i of MOTU relative abundances, with $p_i > 0$ & $\sum_i p_i = 1$, the MOTUs diversity of a given unit is calculated as :

$$\begin{cases} {}^{q}\mathrm{D}(\mathrm{P}) = (\sum_i p_i^q)^{1/(1-q)} & \text{if } q \neq 1 \\ {}^{1}\mathrm{D}(\mathrm{P}) = exp(-\sum_i \times ln(p_i)p_i) & \text{if } q = 1 \end{cases} \tag{5.1}$$

The index is a function of a parameter q, which varied between 0 and ∞ and reflects the effect of MOTUs abundance on the diversity estimation. If q is high, then ${}^{q}\mathrm{D}(\mathrm{P})$ depends more on very abundant species and the less on rare species. It further generalizes classical diversity metric into a single formula : ${}^{0}\mathrm{D}(\mathrm{P})$ is equal to MOTU richness, ${}^{1}\mathrm{D}(\mathrm{P})$ to the exponential of Shannon entropy and ${}^{2}\mathrm{D}(\mathrm{P})$ to the inverse of Simpson.

To characterize the diversity turnover between each hierarchical levels of the meta-community, we used a multiplicative nested diversity decomposition framework [Pavoine et al., 2005; Tuomisto, 2010]. It possesses important properties [Baselga, 2010; Chalmandrier et al., 2015a] that can be useful for diversity decomposition [Jost, 2007]. We were interested in only four diversity measures returned by this decomposition that are detailed below together with their relevant properties.

First, at the scale of the communities identified as community *ij* (community *j* in site *i*), we were interested in two measures. (1) the community α-diversity, $\alpha_{ij}(q)$; (2) the within-community sample heterogeneity, $\beta_{ij}(q)$, as the ratio of $\alpha_{ij}(q)$ and the average diversity within samples of community *ij*.

We defined the vectors P_{ijk} of MOTU relative abundance in the sample k of community *ij* and the vectors P_{ij} of MOTU mean relative abundance across the samples of community *ij* and calculated the aformentionned measures :

$$\alpha_{ij}(q) = {}^{q}\mathrm{D}(\mathrm{P}_{ij}) \tag{5.2}$$

$$\beta_{ij}(q) = \begin{cases} {}^{q}\mathrm{D}(\mathrm{P}_{ij}) / [\frac{1}{\mathrm{S}} \sum_k^q \mathrm{D}(\mathrm{P}_{ijk})^{1-q}]^{1/(1-q)} & \text{if } q \neq 1 \\ {}^{1}\mathrm{D}(\mathrm{P}_{ij}) / exp[\frac{1}{\mathrm{S}} \sum_k log({}^{1}\mathrm{D}(\mathrm{P}_{ijk}))] & \text{if } q = 1 \end{cases} \tag{5.3}$$

Second at the scale of the meta-community, we calculated (3) the β-diversity across sites $\beta(q)$, : as the ratio between the diversity at the scale of the landscape and the mean diversity within site ; (4) the average within-site heterogeneity in the landscape, : $\sigma(q)$, as the ratio of the average diversity of the 10 sites across the landscape and the average sample diversity within sites across the landscape.

We defined the vector P of MOTU mean relative abundance across all samples in the landscape, the vectors P_i of the MOTU mean relative abundance across samples in site i ; and the vectors P_{ijk} of MOTU relative abundance in the sample k of community j in site i. We calculated $\beta(q)$ and $\sigma(q)$ as :

$$\beta(q) = \begin{cases} {}^{q}\mathrm{D}(\mathrm{P}) / [\frac{1}{10}\sum_{i}^{q} \mathrm{D}(\mathrm{P}_i)^{1-q}]^{1/(1-q)} & \text{if } q \neq 1 \\ {}^{1}\mathrm{D}(\mathrm{P}) / exp[\frac{1}{10}\sum_{i} log({}^{1}\mathrm{D}(\mathrm{P}_i))] & \text{if } q = 1 \end{cases} \tag{5.4}$$

$$\sigma(q) = \begin{cases} [\frac{1}{10}\sum_{i}^{q} \mathrm{D}(\mathrm{P}_i)^{1-q}]^{1/(1-q)} / [\frac{1}{\mathrm{S}*20}\sum_{ijk}^{q} \mathrm{D}(\mathrm{P}_{ijk})^{1-q}]^{1/(1-q)} & \text{if } q \neq 1 \\ exp[\frac{1}{10}\sum_{i} log({}^{1}\mathrm{D}(\mathrm{P}_i))] / exp[\frac{1}{\mathrm{S}*20}\sum_{ijk} log({}^{1}\mathrm{D}(\mathrm{P}_{ijk}))] & \text{if } q = 1 \end{cases} \tag{5.5}$$

$\beta(q)$ is set between 1 and 10 ; $\beta_i j(q)$ is set between 1 and S and $\sigma(q)$ between 1 and $2 \times \mathrm{S}$ [Chalmandrier et al., 2015a; Jost, 2007]. To be able to compare these estimates across S values, we standardize them to range between 0 and 1 [Chao et al., 2012] :

$${}^{Std}\beta = \frac{\beta(q) - 1}{10 - 1} \qquad {}^{Std}\sigma(q) = \frac{\sigma(q) - 1}{2\mathrm{S} - 1} \qquad {}^{Std}\beta_{ij}(q) = \frac{\beta_{ij}(q) - 1}{\mathrm{S} - 1} \tag{5.6}$$

Repetitions

These operations were repeated for S varying between 2 and the maximum possible sampling effort (see Table 1). For each S value, the analysis was repeated 50 times to account for the variability induced by the rarefaction step and the random selection of S samples. In each repetition, the diversity estimates were computed for eleven values of q spread regularly between 0 and 5.

Estimation of sufficient sampling effort

For each lineage, we estimated the sufficient sampling effort for $\beta(q)$ and each $\alpha_{ij}(q)$. Visual analysis of their relationship with S revealed an increasing saturating curve with $\alpha_{ij}(q)$ and a decreasing saturating curve with $\beta(q)$. We modeled these relationships with a generalized additive model with a smooth term.

We considered that the "true" estimate of the diversity value was the one modeled for a maximum sampling size and the sufficient sampling effort was the minimum number of samples to obtain a diversity value "close" to the true estimate. The closeness was defined as 5% of the range on which the modeled curve varied. This method assumed that our maximum sampling effort was sufficiently large, i.e. that adding more samples did not change results anymore at a certain point. However, our estimated sufficient sampling sizes were sometimes close to the maximum sampling size potentially indicating that maximum sampling sizes were not high enough. In these cases, we visually checked if the relationship was saturating.

Synthesis

First we compared the $\beta(q)$ and $\sigma(q)$ across q values and the five lineages. The aim was to describe the turnover of communities across the elevational gradient ($\beta(q)$) and the

local turnover within sites ($\sigma(q)$) to better understand the ecological differences between the studied lineages.

We then related the sufficient sampling size of α-diversities (α_{ij}) to three explanatory factors using a linear model with two-ways interactions (n = 1100) : the within-community sampling heterogeneity (β_{ij}), q and the lineage. Similarly we related β-diversity (β) to three explanatory factors using a linear model this time without accounting for interactions due to the lower amount of data (n = 55) : the within-site sampling heterogeneity ($sigma$), q and the lineage.

2.6 Accessing the impact of taxonomic uncertainty on MOTU phylogenetic α-diversities

Dataset

We only analysed Fungi and Viridiplantae data because we only had a phylogeny for these lineages. We used the maximum sampling size for both datasets (19 samples per plot for Fungi and 21 samples per plot for Viridiplantae). We removed four MOTUs from the Viridiplantae dataset to reduce it to Mesangiospermae : these MOTUs were infrequent, rare and associated with long branches that were likely to distort the estimation of phylogenetic diversity.

Construction of the MOTU phylogeny

Phylogenies - A phylogeny of alpine plants was built using the workflow proposed in Roquet et al. [2013] with DNA sequences downloaded from Genbank. We retrieved the Fungi phylogeny from James et al. [2006]. The two phylogenies have different resolutions : the phylogeny of alpine plants was a genus-level phylogeny that was exhaustive of the local alpine flora while the Fungi phylogeny was a supertree only representative of deep divergences. We transformed it into an ultrametric tree using the R-function chronos [Paradis et al., 2004].

Classification data â Complete classification data was retrieved for each MOTU assignation and each tip of the two phylogenies from the NBCI taxonomic database using the R-library taxize [Chamberlain and Szöcs, 2013]. Overall, the taxonomic assignation of MOTU was similar for both Viridiplantae and Fungi : a good proportion of MOTU were assigned to genus-level or above (68% for Fungi and 60% for Viridiplantae) and a small proportion were assigned below the family level (12% for Fungi and 3% for Viridiplantae).

Algorithm â MOTUs order were added sequentially to their phylogeny to the highest possible resolution, if necessary at random. After randomization of the MOTUs order, the procedue followed the following steps.

1. Tips referring to the taxonomic assignation of the MOTU were identified. If no tips were found (it only concerned those Fungi MOTUs that had a better taxonomic as-

signation than what was available from the phylogeny), the taxonomic rank of the MOTU was lowered until corresponding tips were found in the phylogeny.

2. We defined the smallest monophyletic subtree that encompasses the set of selected tips and choose at random a tip or a node from it.

3. We stitched the MOTU to the chosen tip. If it was a node, we stitched it at random on the branch below it.

4. We repeated this procedure for each MOTU.

Analysis

We used two phylogenetic diversity indices on the resulting phylogenies and the MOTU-by-site matrices : the Faith index [Faith, 1992] and the equivalent number of Rao's quadratic entropy [Rao, 1986]. Both indices are Hill numbers that incorporate phylogenetic information [Chao et al., 2010] and correspond to q equal to 0 and q equal to 2, respectively.

We defined $\mathrm{P_B} = \{p_b\}$ and $\mathrm{L_B} = \{\mathrm{L}_b\}$, the vectors of the phylogeny branch abundances and lengths. Branch abundance is calculated as the summed abundance of its descending tips. T is the total branch length separating the phylogeny tips from the root. Note that the two phylogenies were ultrametric.

$$ {}^{0}\mathrm{D}(\mathrm{P_B}, \mathrm{L_B}) = \sum_b \frac{\mathrm{L}_b}{\mathrm{T}} \tag{5.7} $$

$$ {}^{2}\mathrm{D}(\mathrm{P_B}, \mathrm{L_B}) = (\sum_b \frac{\mathrm{L}_b}{\mathrm{T}} \times p_b^2)^{-1} \tag{5.8} $$

Any values of q can be theoretically studied but exploring a large range of values is computationally very demanding, especially when large phylogenies are involved.

As phylogenetic α-diversities are correlated to the number of MOTUs, we used a tip-shuffling null model and based on the resulting null distributions calculated the Z-score of the α-diversities. Z-scores were calculated as the observed α-diversity minus the mean of the distribution divided by the standard deviation of the null distribution. Resulting Z-scores are independent of the number of MOTUs.

As the stitching of MOTUs on the phylogeny is partially random, the analysis was repeated 100 times for both Fungi and Mesangiospermae and both diversity indices. We then accessed how the Z-scores of communities changed across repetitions by calculating the pairwise Spearman correlation between ranks.

3 Results

3.1 Factors influencing the sufficient sampling size

α-diversity

Sufficient sampling varied according to the lineage and the q value (Figure 5.2). For all five lineages, sufficient sampling size decreased sharply when q increases, and was dependent on the lineage considered (Supplementary materials, Table 5.2). When diversity was expressed as the number of MOTUs, sufficient sampling size was close to the maximum sampling size for all lineages : Archea (13.7) Bacteria (17.4), Fungi (17.0), Eucaryota (16.7), Viridiplantae (18.1). Visualization of the relationships confirmed that the estimation of diversity did not converge despite the sampling effort. When diversity was calculated with the inverse of Simpson or any Hill number that gave more weight to dominant MOTUs ($q \geq 2$), less than 15 samples per plot were necessary to estimate α-diversity. Fungi were peculiar compared to the other lineages in that a higher number of samples was required for a given value of q compared to the other lineages.

Sufficient sampling size to estimate community α-diversity was positively related to the underlying within-community heterogeneity ${}^{Std}\beta_{ij}(q)$, the relationship being dependent on both lineage and value of q (Supplementary materials : Table 5.2). Fungi had a distinct pattern from the other lineages in that it required overall a higher number of samples and that it showed interactions that were significantly different from the other lineages (Table 5.2). Probably, this mostly arose from the high within-site heterogeneity for high values of q that was unique to Fungi.

β-diversity

As for α-diversity, sufficient sample size to estimate β-diversity was negatively related to the q parameter and positively related to the average within-site heterogeneity of samples (Figure 5.2, 5.3 ; Supplementary materials : Table 5.3). When estimates of β-diversity were based on MOTUs richness, values ranged from 17.24 samples per plot for Viridiplantae to 10.23 samples per plot for Archea. Visualization of the relationships confirmed that the -diversity estimation converged only for Archea. When diversity was calculated with the inverse of Simpson or any Hill number that gave more weight to dominant MOTUs ($q \geq 2$), less than 10 samples per plot was required.

3.2 Diversity profiles of β and σ across lineages

The diversity profiles describing the relationship between diversity patterns and the q parameter revealed contrasting patterns depending on the lineage and the importance of abundance weight, i.e. the value of the q parameter (Figure 5.4). When diversity was expressed as the number of MOTUs ($q = 0$), Archea was the clade that had the strongest

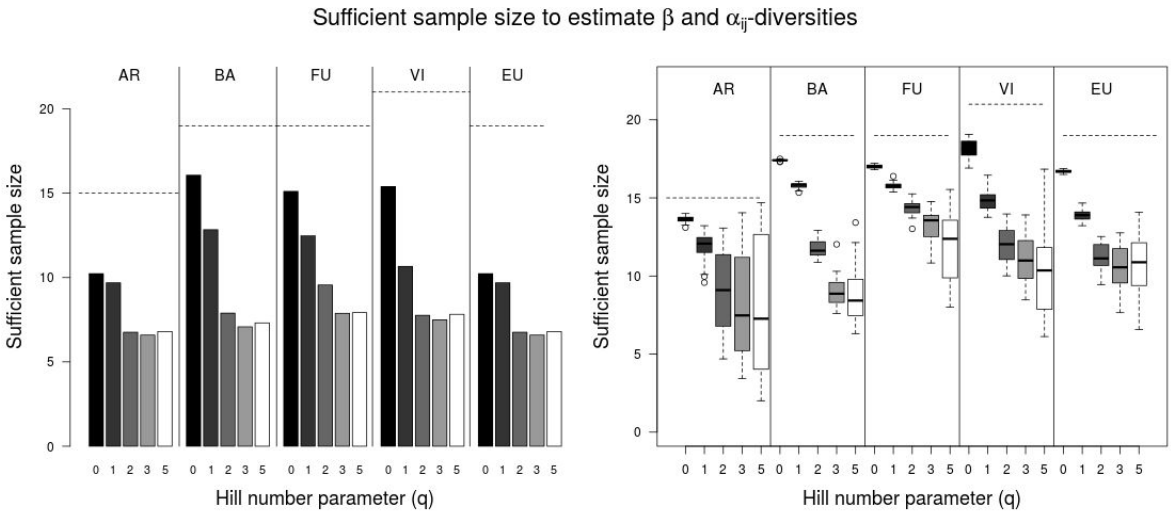

FIGURE 5.2 – Sufficient sample size to estimate β-diversity and α-diversity of the 20 communities (right). In each panel, from left to right are displayed the results for Archea (AR), Bacteria (BA), Fungi (FU) Viridiplantae (VI) and Eucaryota (EU). The sufficient sampling size is displayed for five values of Hill number parameter q (0, 1, 2, 3, 5). The gray scale represents the q parameter (black being 0 and white being 5). Horizontal dotted lines mark the maximum sampling size for each lineage.

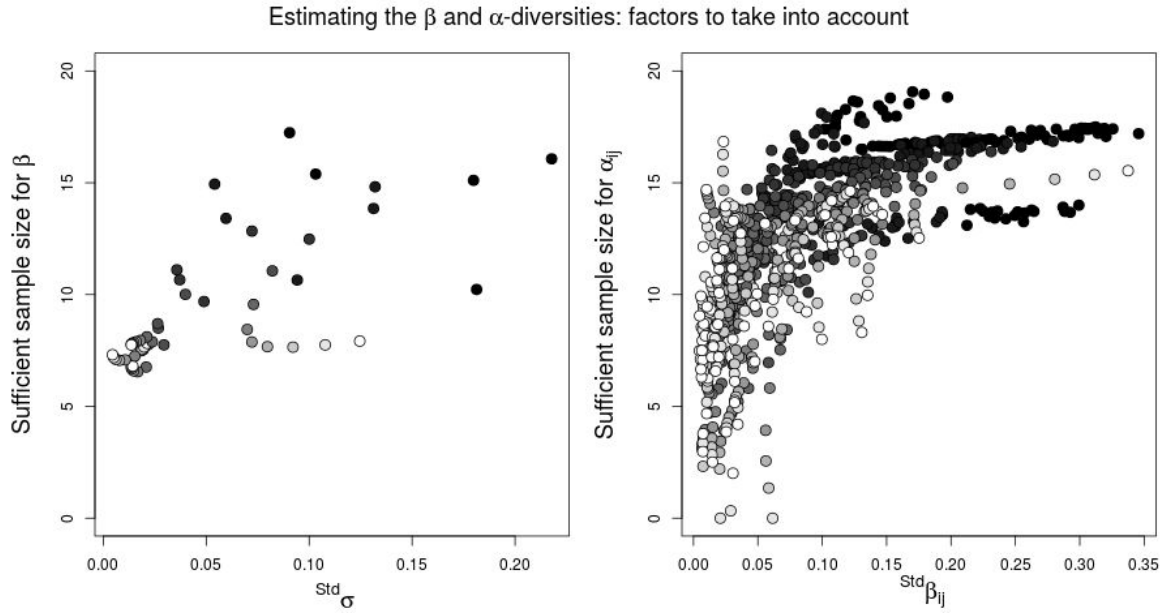

FIGURE 5.3 – Influence on the β-diversity sufficient sampling size of average within-site sample heterogeneity (left) and influence on community α-diversity sufficient sampling size of the within-community heterogeneity (right). All lineages are represented. The gray scale represents the q parameter (black being 0 and white being 5)

turnover across sites (β on average equal to 3.37) followed closely by Fungi, then Bacteria, Viridiplantae and finally Eucaryota that had the lowest turnover (1.94 on average). When focusing on the turnover within communities (within-site sample heterogeneity), microbial lineages had the strongest turnover (Bacteria : ${}^{Std}\sigma = 0.30$, Archea : ${}^{Std}\sigma = 0.25$ and Fungi : : ${}^{Std}\sigma = 0.23$) while Eucaryota and Viridiplantae had the lowest turnover (respectively ${}^{Std}\sigma = 0.16$, Archea : ${}^{Std}\sigma = 0.15$). The picture changed drastically when q increased. β-diversity strongly decreased showing that there were abundant MOTUs spreading out across the gradient therewith homogenizing communities and reducing β-diversities. For $q = 5$, all lineages had a low turnover between 1.1 (Bacteria) and 1.47 (Fungi).

For all lineages but Fungi, within-site sample heterogeneity showed a similar pattern. For high q values, e.g. $q = 5$, samples within plots were barely distinguishable from each other (${}^{Std}\sigma$ set between 0.0085 for Bacteria and 0.04 for Eucaryota). Fungi was particular in that it maintained a high within-site sample heterogeneity both at low and high values of q. It reached a minimum for a value of q between 2 and 3 and increased to a value of 0.19 for $q = 5$.

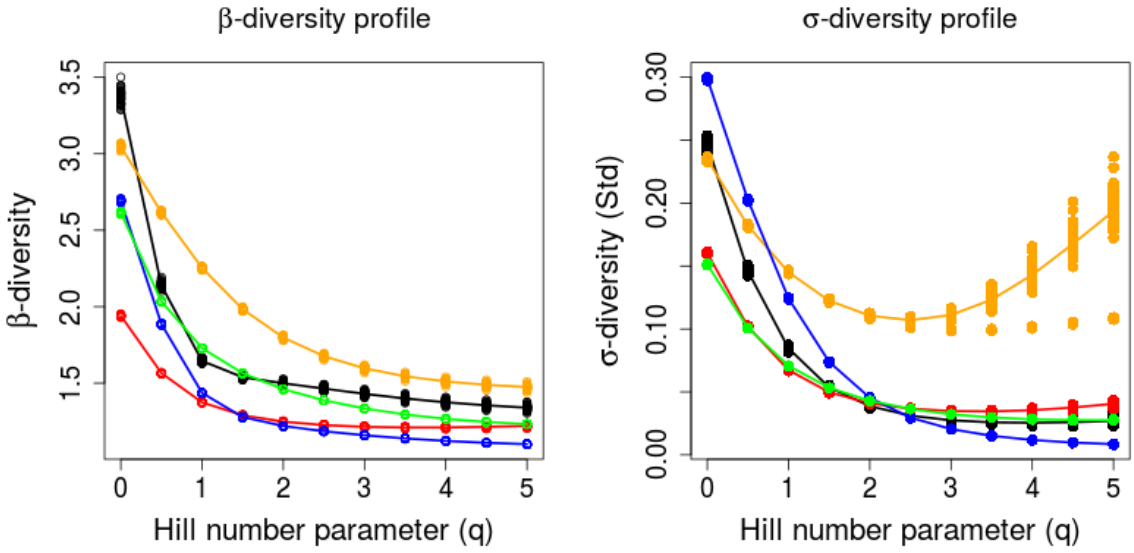

FIGURE 5.4 – Diversity profile of the β-diversity-diversity and the average within-site heterogeneity σ as a function of the Hill parameter q and the lineage considered. Colors represent the lineage : Archea (black), Bacteria (blue), Fungi (orange), Viridiplantae (green) and Eucaryota (red).

3.3 Taxonomic assignment and phylogenetic diversity

Ranking of communities across repetitions remained consistent regardless of the lineage and the used diversity indices despite taxonomic uncertainties (Figure 5.5). More quantitatively, Mesangiospermae ranking were highly correlated across repetitions when calculated with Faith index (average of correlation coefficients : 0.85 with a standard deviation of 0.080) and even more so when calculated from Rao's quadratic entropy (average of 0.97 with a standard deviation of 0,016). Fungi rankings were less consistent with Faith

index (average correlation of 0.72 with a standard deviation of 0.18) but not with Rao's quadratic entropy (average correlation of 0.96 with a standard deviation of 0.015).

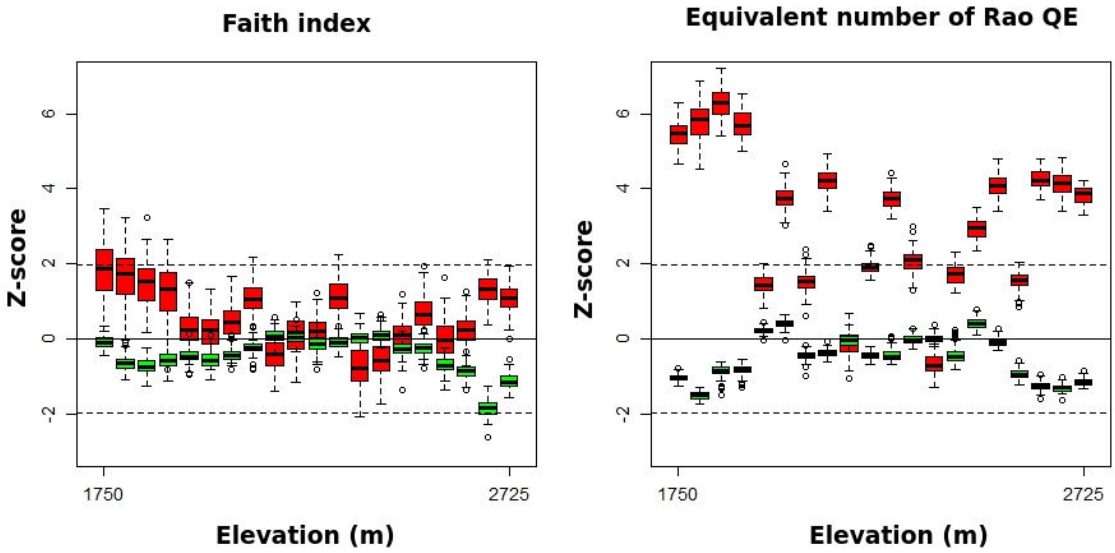

FIGURE 5.5 – Z-scores of Fungi (red) and Mesangiospermae (green) phylogenetic diversity. Left panel was obtained with Faith index which do not take into account MOTUs relative abundance and the right panel with the equivalent number Rao's quadratic entropy which takes into account MOTUs relative abundance. Community plots are ordered by increasing elevation.

4 Discussion

4.1 Sampling size : the importance of underlying community heterogeneity

Our study shows how the ecology of soil biota intersects with the sampling design of meta-barcoding data. The five considered lineages differed markedly in diversity turnover across spatial scales in our study sites and this impacted the sampling effort required to obtain robust estimates of α-diversity and β-diversity. The choice of diversity metric was critical as the required sampling effort was heavily dependent on this choice. Our results go in the direction of the work of Haegeman et al. [2013] who showed that the richness of a sample cannot be reliably estimated as rare MOTUs cannot reliably be detected. Accordingly, our study demonstrates empirically that multiplying the number of samples to get a more representative account of community richness may not improve the estimates of local richness.

While we had expected that zooming out to a large scale would average out the effect of local heterogeneity, the estimation of β-diversity from richness indices also failed to converge with increasing sampling effort. This under-sampling typically led to the overestimation of β-diversity. An intuitive reasoning for this is that under-sampling conflates

the turnover across sites (β) with local spatial turnover. Choosing a Hill number with a high value of q, such as the inverse of Simpson, which takes relative abundances into consideration, resulted in much lower sufficient sampling size for reliable estimates of α and β-diversities (inferior to 15 per plots for α and 10 for the β).

Regardless of the lineage and the parameter q, the differences in sufficient sampling size were explained by the underlying turnover between samples. Typically local turnover decreased when relative abundance were taken into account for all lineages (Figure 5.4) showing that rare species are also infrequent across samples and generated a high local heterogeneity while dominant species were more widespread. Consequently sufficient sample size was decreasing with increasing weight given to the dominant species, i.e. with increasing q.

There were differences between lineages : Archea and Fungi stood out. Archea was the only lineage for which we obtained a stable estimation of the β-diversity even when relative abundances were ignored ($q = 0$). This was paradoxical as the underlying heterogeneity within sites was not low (0.18) and comparable to the other lineages. Archea was also the lineage that displayed the highest β-diversity. Archea are known to respond more strongly to abiotic conditions than Bacteria and Fungi in alpine ecosystems [Zinger et al., 2011], we can thus hypothesize that because Archea had a stronger turnover across the gradient, estimates were less affected by the sampling uncertainty caused by within-site local heterogeneity.

Within-site sample heterogeneity was markedly higher for Fungi than for the other lineages and, further contrasting with the other lineages, it increased for high values of q. We interpreted this as follows : for low values of q, the high within-site sample heterogeneity revealed that rare Fungi MOTUs made up the majority of turnover between samples. For intermediate values of q, samples appeared the most homogeneous as only dominant and intermediate MOTUs are taken into account. However unlike the other lineages, there was probably marked shifts in the dominance hierarchy between these MOTUs across samples which explained the high within-site sample heterogeneity for high values of q. Consequently the estimation of Fungi α-diversities required a higher number of samples, even when the parameter q was high.

The study of biodiversity patterns across soil biota in terms of ecological processes has just started and more studies are certainly needed. However, we would like to highlight that our results confirm well with the work by Zinger et al. [2011]. Comparing alpine grassland Archea, Bacteria and Fungi communities, they found that Fungi communities were mainly driven by biotic interactions with plants. Such processes would well explain our observed strong shifts in Fungi diversity at a small spatial scale, leading to a less robust estimation of local diversity when low sample size is low.

4.2 Limited impact of taxonomic uncertainty

Phylogenetic Z-scores were consistent regardless of the diversity index and the lineage despite a taxonomic assignation below genus-level for about 40% of the MOTUs. It was further surprising that Fungi phylogenetic diversity was so consistent despite the use of a phylogeny that was much less resolved than the plant phylogeny although Faith phylogenetic diversity was a bit less robust for Fungi than Mesangiospermae. This may be due to the important number of rare Fungi MOTUs that are stitched on an imprecise phylogeny. The effect of this uncertainty was however limited and did not impact much the pattern of phylogenetic diversity across elevation.

This consistency was probably due to the fact that phylogenetic diversity estimates are mostly dependent on deep phylogenetic divergences, as the amount of MOTUs that were not identified above the family level was limited, the phylogenetic diversity remained robust to the random placement of MOTUs.

4.3 Studying MOTUs diversity patterns : a question of sampling and objectives

Our work showed that richness and richness turnover across gradients cannot be accurately estimated even with an important sampling effort because of the importance of local community turnover. Any other abundance-weighted diversity estimates ($q \geq 1$) was more robust to sampling effort. However indices are not a magical tool : choosing one in particular sets the objective of the study and changing indices can lead to changing results. By focusing on a high value of q, a strong focus is put on dominant species thus ignoring rare specimens that can have important functions in the ecosystem [Mouillot et al., 2013] or may reveal particular community assembly rules [Chalmandrier et al., 2015b].

In the end, the choice of a diversity index is a compromise between the objective of the study and on the contingency of the sampling design that may not allow the scientist to choose any possible diversity index. Our study results are probably specific to the alpine ecosystem, but they do provide some more general guidelines about the intensity of the sampling effort that is required depending on whether the studied lineage is prone to local turnover or not. Our study also shows that phylogenetic diversity indices can be robustly estimated despite taxonomic uncertainty and lack of resolution of phylogeny tips. We however recommend the use of the described algorithm to explicitly test the robustness of phylogenetic patterns, especially if the objective of the study is to study fine-scale patterns within lineages where the impact of taxonomic uncertainty may be more marked than at a large phylogenetic scale.

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6 Supplementary materials

6.1 Identification and removal of false sequences for the *tnrL* marker

Methods

Based on the composition of positive controls of plant extract, we were able to model the probability of a sequence to be a false sequence (contaminant, PCR error...) vs. a true sequence utilizing information on sequence abundances and frequencies across sample replicates. Based on the resulting probability estimates we filtered out some sequences from the Viridiplantae sample-by-MOTUs table that were likely to be false sequence.

First we modeled the probability p_{ijk} of the MOTU i in the replicate k of sample j to be a true sequence using a generalized linear model with a single explanatory variable x_{ijk}. We tested three different covariates describing the abundance of MOTU i in the replicate k of sample j : its number of reads (NbSeq), N_{ijk} ; its relative abundance (AbRel) : $\frac{\mathrm{N}_{ijk}}{\sum_i \mathrm{N}_{ijk}}$; and its relative abundance after log-transformation of the number of reads (logAb) : $\frac{log(\mathrm{N}_{ijk}+1)}{\sum_i log(\mathrm{N}_{ijk}+1)}$. p_{ijk} was modeled using a binomial generalized model :

$$\mathrm{logit}(p_{ijk}) = a + b \times x_{ijk} \tag{5.9}$$

Once the parameters a and b were estimated, we calculated the probability p_{ij} of the MOTU i in the sample j to be a true sequence with the formulaÂ :

$$p_{ij} = 1 - \prod_k (1 - p_{ijk}) \tag{5.10}$$

The rational behind this is that the probability of MOTU i in sample j to be a true sequence is equal to the probability of being a true sequence in at least one of the replicates.

We implemented a repeated split-sample procedure to evaluate the performance of each of the three models (i.e. based on the three different explanatory variables) and determined the optimal cut-off value to separate true and false sequences based on pij. We did this by repeating model fitting 500 times for randomly selected 70% of the initial data (while maintaining the ratio of false and true sequences constant) and then evaluated on the remaining 30% the sensitivity, specificity and the true skill statistic (TSS ; Allouche et al. [2006]) of the models. Sensitivity (resp. specificity) describes the proportion of true sequences (resp. false sequences) that are identified as such by the model. The TSS aggregate both characteristics into a single index that has a range of -1 to +1, with -1 and +1 representing systematically wrong predictions and systematically right predictions, respectively, and 0 representing a random fit. In each repetition, we determined the optimal cutoff as the value that maximize TSS.

Results

The models didn't have marked differences (Figure 5.6) in terms of performance and all performed well (mean TSS equal to 0.930). Nevertheless, the model based on the number of reads was on average the least efficient in terms of TSS (0.920), this result was due to both a lower sensitivity and specificity (Figure 1). The model based on the relative abundance of reads after log-transformation and the model based on relative abundance were equivalent in terms of TSS, sensitivity and specificity (Figure 1).

Fitting trials on the field samples revealed that the model based on the relative abundance of reads after log-transformation was the most stringent of the three (Figure 5.7). It removed a higher number of sequences per sample (on average 94.0 against 34.3 for the RelAb model and 33.9 for the NbSeq model), a higher number of MOTUs per sample (on average 21.6 against 16.9 for the RelAb model and 16.6 for the NbSeq model) and a higher number of MOTUs were removed from the whole dataset (311 against 250 for the RelAb model and 271 for the NbSeq model).

Based on this observation, we took the most efficient and conservative approach and selected the logRelAb model.

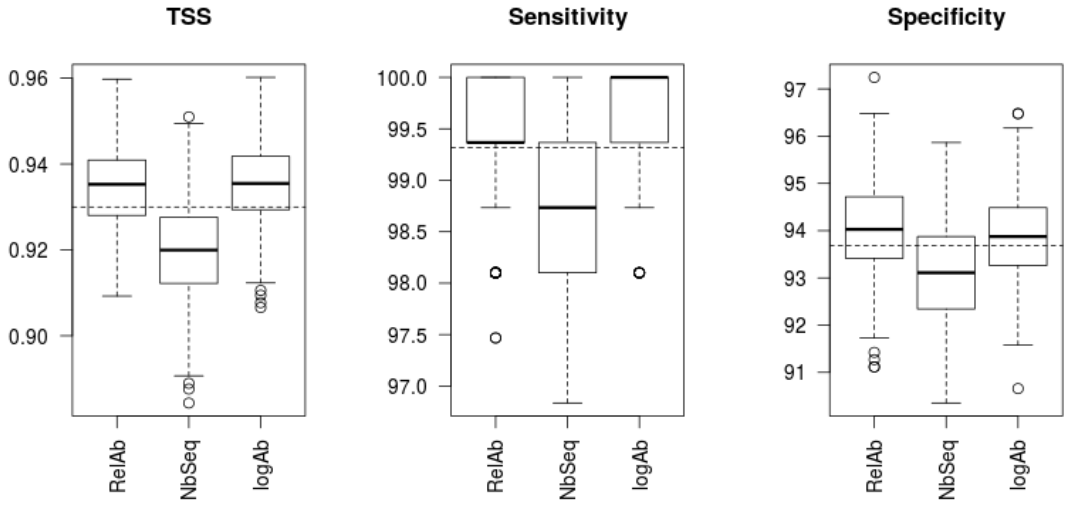

FIGURE 5.6 – Efficiency of relative abundance of sequences (RelAb), number of sequences (NbSeq) and relative log-transformed number of sequences (logAb) per sample as cofactors to model false sequences in positive controls. From left to right are displayed the True Skill statistics, the sensitivity and the specificity of the models.

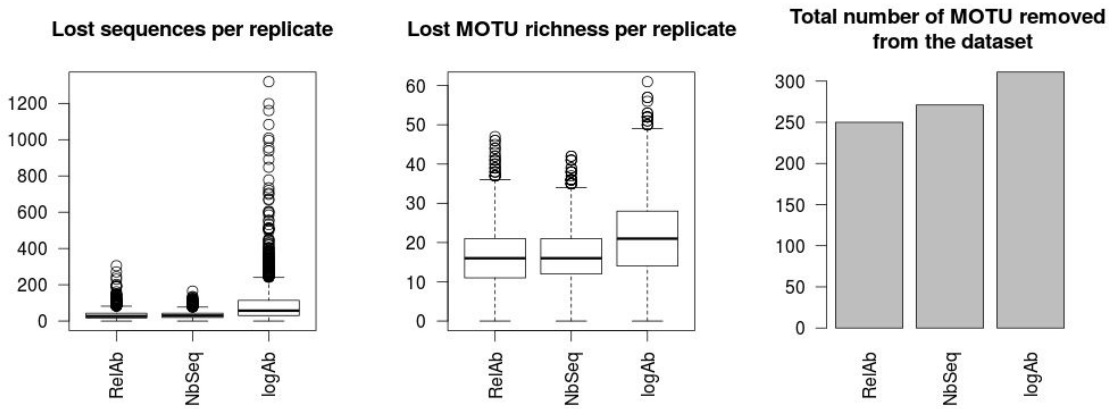

FIGURE 5.7 – Efficiency of relative abundance of sequences (RelAb), number of sequences (NbSeq) and relative log-transformed number of sequences (logAb) per sample as cofactors to model false sequences in positive controls. From left to right are displayed the True Skill statistics, the sensitivity and the specificity of the models.

6.2 Predictors of α and β-diversities sufficient sampling size

Coefficient	Estimate	P-value
Intercept	9.30	<0.0001
Lineage (BA)	2.80	<0.0001
Lineage (FU)	7.94	<0.0001
Lineage (VI)	2.08	<0.0001
q	-0.74	<0.0001
${}^{Std}\beta_{ij}$	7.85	<0.0001
q : ${}^{Std}\beta_{ij}$	0.39	<0.0001
q : Lineage(FU)	-24.0	<0.0001
${}^{Std}\beta_{ij}$: Lineage(FU)	1.31	<0.0001
${}^{Std}\beta_{ij}$: Lineage(VI)	1.67	<0.0001
${}^{Std}\beta_{ij}$: Lineage(EU)	2.70	<0.0001

TABLEAU 5.2 – Coefficients of the linear model predicting sufficient sampling size of α-diversities. Lineage dependent coefficients are set in contrast to Archea ; only significant coefficients are displayed (p-value < 0.05)

Coefficient	Estimate	P-value
Intercept	8.68	<0.0001
Lineage (BA)	1.57	0.009
Lineage (VI)	2.39	0.0001
Lineage (EU)	1.73	0.004
q	-0.87	<0.0001
$^{Std}\sigma$	14.47	<0.0001

TABLEAU 5.3 – Coefficients of the linear model predicting sufficient sampling size of α-diversities. Lineage dependent coefficients are set in contrast to Archea ; only significant coefficients are displayed (p-value < 0.05)

Quatrième partie

Discussion

Chapitre 6

Discussion

> « *It is hard to convey five-dimensional ideas in a language evolved to scream defiance at the monkeys in the next tree.* »
>
> Terry Pratchett - Darwin's watch

Le but de l'étude des patrons de diversité des communautés est de comprendre les règles d'assemblage qui contraignent la diversité des communautés. Dans une perspective où la compréhension de ces règles peut permettre de mieux appréhender les impacts des changements globaux sur la biodiversité, il est essentiel de pouvoir étudier en détail les nombreux mécanismes écologiques qui en sont à l'origine. Les différents travaux de ma thèse bien que relativement indépendants les uns des autres ont visé cet objectif et sont articulés autour de la même démarche analytique : reprendre la question simple qui est au cœur de l'analyse des patrons de diversité : "est-ce que les communautés sont des échantillons aléatoires de la région ?", identifier les hypothèses de travail qui y sont associées, leurs implications en termes écologiques et les remettre en cause.

À ce titre, les résultats de ma thèse s'organisent autour de deux axes sur lesquels je souhaite revenir dans cette discussion. Le premier est la réponse à la question "qu'a t-on appris sur l'assemblage des communautés herbacées des Alpes ?". Dans un premier temps, je vais revenir sur les différentes règles d'assemblage qui ont été décrites tout au long de cette thèse. Les différents travaux de ma thèse se sont focalisés principalement sur la diversité fonctionnelle des communautés herbacées alpines (Chapitres 1, 2, 3, Thuiller et collab. [2014]) mais également sur leur diversité phylogénétique (Chapitres 3, Thuiller et collab. [2014]). Le but de cette première partie est de les mettre en perspective afin de dessiner une image cohérente de la façon dont les règles d'assemblage produisent des patrons de diversité complexes à différentes échelles spatiales qui diffèrent selon la facette étudiée (fonctionnelle/phylogénétique) et de façon générale permette de mieux comprendre le fonctionnement des écosystèmes alpins.

Dans un second temps, j'aborderai les perspectives méthodologiques de mon travail,

en particulier la façon dont la remise en cause des hypothèses liées au modèle nul (Chapitre 1, 2) et aux indices de diversité (Chapitres 3, 4, 5) peut complexifier mais aussi améliorer l'analyse des patrons de diversité des communautés.

1 Traits fonctionnels et phylogénie : des dimensions complémentaires de la niche

Un des objectifs de ma thèse était d'étudier en parallèle les diversités fonctionnelles et phylogénétiques des communautés. Fondamentalement, par l'utilisation des traits fonctionnels et de phylogénie dans les patrons de diversité, on cherche à quantifier la similarité écologique entre espèces. En fait, ce sont tout deux des proxys quantifiant des axes de niches abstraits difficiles à évaluer [MOUQUET et collab., 2012]. En première approximation, cela pourrait laisser supposer que ces deux types de diversité sont censés quantifier la même chose. En conséquence, leur efficacité respective pour prédire le fonctionnement des écosystèmes [FLYNN et collab., 2011] ou de savoir si la diversité phylogénétique peut être utilisée comme un proxy, potentiellement peu coûteux, de la diversité fonctionnelle (ex. BERNARD-VERDIER et collab. [2013]; PERRONNE et collab. [2014]).

Ces études concluent en générale que diversité fonctionnelle et phylogénétique ne sont pas comparables et mes travaux ne font pas exception. Dans le souci d'apporter ma pierre à l'édifice de l'analyse comparative entre diversité fonctionnelle et phylogénétique des communautés, je propose de commenter mes résultats pour chacune de ces deux entités dans le but de les intégrer ensemble.

1.1 Diversité fonctionnelle : l'empreinte des gradients environnementaux à de multiples échelles

Influence du filtre climatique à large échelle spatiale

La conclusion première de mon travail sur la diversité fonctionnelle est le lien étroit entre les traits fonctionnels et les grands gradients environnementaux des Alpes. Ainsi dans le Chapitre 2, tout les traits étudiés étaient dépendants des gradients sous-jacents via le trait moyen des communautés et via la diversité des communautés (Figure 2.6 et 2.7). De même, la diversité fonctionnelle des communautés changent de façon importante dans la Guisane quelque soit la paramétrisation de l'indice de diversité utilisé et que cela était explicitement lié à des différences de conditions abiotiques (Chapitre 3). À cet égard, mes travaux de thèse sont en concordance avec la littérature sur les relations entre diversité fonctionnelle des communautés végétales et grands gradients des Alpes [DE BELLO et collab., 2013; KÖRNER, 2003].

Une contribution nouvelle de mon travail au domaine tient surtout à l'étude des patrons de diversité des traits isotopiques foliaires qui n'ont pas été beaucoup étudiés dans

le contexte des communautés végétales le long de gradients alpins. À cet égard, le ratio δ^{15}N (Figure 2.6) n'a pas fait l'objet d'une étude spécifique mais présente des perspectives de recherche intéressantes. Les résultats de ce chapitre suggèrent ainsi que le ratio isotopique foliaire δ^{15}N diminue avec la baisse des stocks d'azote. Cette diminution du trait était également associée avec une augmentation de sa diversité au sein des communautés allant a contrario du patron fonctionnel général de diminution de la diversité des traits fonctionnels dans les conditions climatiques les plus stressantes. L'interprétation du ratio isotopique foliaire δ^{15}N est compliquée due aux multiples facteurs qui l'influent (type d'azote absorbée, type de mycorhization... HOBBIE et HÖGBERG [2012]) ce qui rend difficile l'interprétation du trait moyen par un profil fonctionnel type. En revanche, l'augmentation de la diversité dans les communautés pauvres en azote est une découverte intéressante car elle suggère que face au manque de ressources il y a une coexistence accrue de différentes stratégies d'absorption de l'azote et donc un partitionnement de niche lié à la diminution de la quantité d'azote dans le sol avec l'altitude (ASHTON et collab. [2010]). Il est probable qu'une approche plus écosystémique permettra de décrypter davantage les mécanismes sous-jacents associés à ce trait, par exemple en mettant à part les Fabaceae, prenant en compte la contenance des différentes sources d'azote dans le sol et utilisant les données de méta-barcoding sur les communautés microbiennes du sol pour mettre en relation explicitement les différents éléments du cycle de l'azote dans ces communautés.

L'importance relative de la variabilité intraspécifique

Un des apports de ma thèse sur la question des traits fonctionnels est l'influence de la variabilité intraspécifique à la diversité fonctionnelle des communautés alpines. S'il était connu que les traits fonctionnels varient de façon plus ou moins prédictibles au sein des espèces en réponse aux gradients [ALBERT et collab., 2010a; BOUCHER et collab., 2013; THUILLER et collab., 2010], il n'était en revanche pas évident que la variabilité intraspécifique soit essentielle à la compréhension de l'assemblage des communautés. Il a été ainsi suggéré qu'elle ne soit nécessaire que dans certains contextes, c'est-à-dire dire à large étendue ou grain spatial [ALBERT et collab., 2011].

Nos conclusions du Chapitre 2 indiquent qu'effectivement la variabilité intra-spécifique n'est pas nécessaire à large échelle spatiale pour détecter la diminution de la diversité fonctionnelle avec l'augmentation du stress climatique mais qu'elle était indispensable à la détection du patron de divergence fonctionnelle à petite échelle spatiale. En cela, l'étude correspond aux attendues. Dans le détail, l'étude des traits fonctionnels pris individuellement (Figure 2.6, 2.7) fourni une explication mécaniste à cela : pour le trait moyen comme pour la diversité, l'inclusion de la variabilité intra-spécifique permet ou accentue la détection de l'influence des gradients ou des composantes de l'échelle spatiale mais ne génère pas de patrons opposés à ce que suggére le patron de diversité fonctionnelle inter-spécifique. Cela suggère que la relation entre gradients, composantes spatiales et traits fonctionne de la même façon entre espèces et au sein des espèces et que

le cas inverse, plus compliqué où les traits au sein des espèces varient différemment que les traits entre espèces, ne s'appliquait pas dans cette étude [KICHENIN et collab., 2013]. Étant donné qu'une étendue spatiale large implique des communautés contenant un plus grand nombre d'espèces et un changement d'espèces plus important le long des gradients, la résolution des données de traits ignorant la variabilité intraspécifique est suffisante pour étudier leur assemblage [ALBERT et collab., 2011].

En revanche à petite échelle spatiale (grain fin et grande étendue), mes travaux suggèrent que la diversité fonctionnelle est également contrainte par des processus écologiques locaux. Les travaux du Chapitre 1 et du Chapitre 2 montrent que l'assemblage fonctionnelle des communautés est relativement stochastique à une petite étendue spatiale lorsque la variabilité intraspécifique n'est pas prise en compte.

Par contre, l'étude du Chapitre 2 met en évidence deux patrons en plus. Le premier est un processus de niche lié à un gradient environnemental secondaire déterminé par la variabilité fonctionnelle intraspécifique. L'origine de ce gradient reste à identifier mais avait pour conséquence des anomalies de température vis à vis du gradient climatique principal. En terme de diversité fonctionnelle, les communautés "anormalement froides" étaient fonctionnellement divergentes lorsque la variabilité intraspécifique était incluse. C'est probablement ce statut "d'anomalie" qui explique l'importance de la variabilité intra-spécifique dans ce contexte : ce gradient n'étant pas structuré spatialement, ces communautés reçoivent probablement un afflux de propagules d'espèces des communautés aux alentours dont l'optimum de niche est éloigné des conditions locales. La persistance de ces individus nécessite alors une déviation de leur trait (par plasticité, ou adaptation très locale) par rapport à leur trait moyen d'espèce en réponse au stress abiotique local.

Le second processus écologique résulte en la différenciation taxonomique et fonctionnelle entre communautés situées dans des environnements abiotiques similaires. Nos résultats suggère que cette différenciation n'est due à des processus de niche liés à des gradients environnementaux contenus au sein des sites [CHOLER, 2005]. L'émergence de ces patchs de végétation pourrait être expliquée en invoquant des contingences historiques [FUKAMI et collab., 2005] : au gré de dynamiques de dispersion des propagules, des communautés localement différenciés ont pu se mettre en place. En ajoutant à les stratégies clonales des espèces alpines et subalpines, on peut supposer que cette différenciation taxonomique et fonctionnelle peut devenir facilement pérenne et favoriser le maintien d'une végétation en patchs.

En conclusion, mes travaux montrent le lien étroit entre traits fonctionnels et gradients environnementaux à petite comme à grande échelle spatiale. À large échelle spatiale, ces gradients excluent certaines espèces des communautés en fonction de leurs traits fonctionnels et génère la forte diversité β le long des gradients environnementaux ainsi que des patrons de diversité α variables selon l'intensité du stress abiotique. Et à

petite échelle spatiale (grain fin, petite étendue), les individus ont également un agencement spatial non aléatoire, avec des patrons de co-occurrence liées à des gradients locaux auquel ils répondent grâce à la plasticité de leurs traits.

1.2 La complexité du patron de diversité phylogénétique

Il est intéressant de constater que si le lien entre diversité phylogénétique et fonctionnement des écosystèmes est régulièrement montré [ANACKER et collab., 2014; CADOTTE et collab., 2012; PELLISSIER et collab., 2013], les études d'assemblage des communautés utilisant la diversité phylogénétique sont parfois moins claires [MÜNKEMÜLLER et collab., 2014], et les travaux de cette thèse suggèrent également des patrons complexes liés à la phylogénie.

Dans le Chapitre 1, l'étude sur des données réelles offrait un résultat clair dans la relation entre diversité fonctionnelle et échelle phylogénétique. En revanche, le modèle Virtcom est incapable de simuler un patron interprétable. Cela indique clairement que nous n'avons pas été capables de modéliser réalistiquement l'évolution d'un trait influençant l'assemblage des communautés. De même le Chapitre 3 suggère que le patron de diversité phylogénétique des communautés végétales de la vallée de la Guisane est à la fois différent et plus complexe que leur patron de diversité fonctionnelle.

De fait, contrairement aux traits fonctionnels qui ont été liés à certaines caractéristiques de la niche écologique des espèces, le lien entre phylogénie et niche est moins évident. En fait, ce lien est intimement lié à la façon dont les différentes dimensions de la niche ont pu évolué dans des environnements qui ne sont pas les principaux axes de niches structurant actuellement les communautés. C'est pourquoi un peu de rétrospective sur l'origine de la végétation des gradients des Alpes (qu'on réduira ici aux Angiospermes) est probablement nécessaire.

Nœuds profonds de la phylogénies des plantes des Alpes

Les Angiospermes ont une relation diversité-latitude marquée [FRANCIS et CURRIE, 2003] ce qui indique que seul une sous-partie des espèces d'Angiospermes ont été capable d'occuper le biome Holarctique dont fait partie le pool régional des espèces des Alpes, probablement grâce à des innovations-clefs pour résister au gel [ZANNE et collab., 2014], cela correspond ainsi à l'idée que les nœuds profonds de la phylogénie des Angiospermes reflète la similarité de niche, mais ici à l'échelle du biome [CRISP et collab., 2009] donc à une échelle spatiale et temporelle très grande. Ces innovations, si elles expliquent les nœuds profonds de la phylogénie, ne sont pas pertinente pour expliquer la structuration des communautés des Alpes sauf si les communautés sont comparées à la flore mondiale des Angiospermes (exemple plus ruminant : CANTALAPIEDRA et collab. [2014]).

L'adaptation au climat alpin

Les milieux alpins sont récents. Ils sont apparus grâce à l'orogénèse des massifs alpins (35-25 MA pour les Alpes) et du refroidissement général nécessaire à la mise en place des gradients climatiques à l'origine de la végétation alpine. Cela donne comme date pour la mise en place des gradients de végétation alpine datant à 10 MA pour la flore de l'Hémisphère nord [NAGY et GRABHERR, 2009]. À l'échelle de la flore régionale des Alpes, l'acquisition d'un caractère "alpin" n'est donc susceptible d'avoir sculpter que les nœuds les plus récents de la phylogénie. Étant donné que la structure phylogénétique des communautés est principalement influencée par les lignées anciennes, le patron phylogénétique des communautés représente principalement l'influence d'un héritage évolutif de ses espèces qui est antérieur à l'émergence des gradients climatiques alpins.

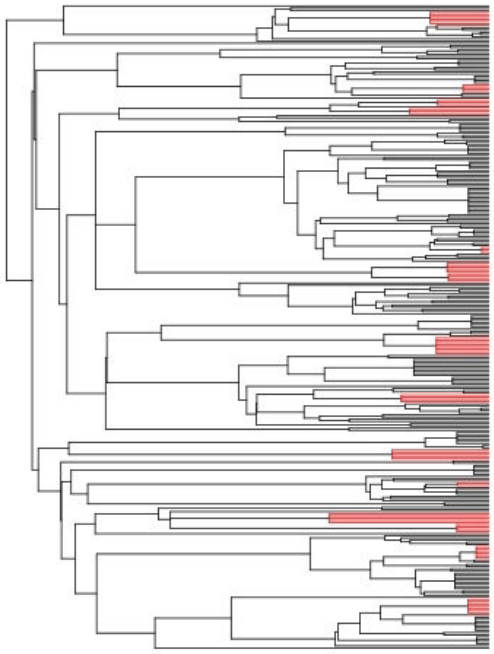

FIGURE 6.1 – Genres "alpins" dans la phylogénie des dicotylédones de la vallée de la Guisane. 30% des espèces de la Flore alpine provient de ces genres. En rouge : Androsace, Artemisia, Astragalus, Cerastium, Campanula, Draba, Gentiana, Pedicularis, Phyteuma, Potentilla, Primula, Ranunculus, Salix, Saxifraga, Viola. [OZENDA, 2002].

En revanche, si seules certaines lignées des plantes des Alpes se sont adaptées à ces gradients, alors la structure phylogénétique des communautés sera affectée par le filtre climatique. Néanmoins, la comparaison de la flore de basse altitude et de haute altitude dans l'Holarctique montrent qu'en fait elles ne sont pas particulièrement distinctes en terme de richesse des grandes familles [NAGY et GRABHERR, 2009; OZENDA, 2002], même si au sein de ces familles existent des genres typiquement "alpins" dispersés dans la phylogénie (Figure 6.1). Au final, la structuration de la flore le long des gradients climatiques est plus probablement le fruit de multiples convergences évolutives au sein des Angiospermes pour s'adapter aux conditions d'altitude [ARAÚJO et collab., 2013] ainsi qu'à la diversification des ces genres alpins [BOUCHER et collab., 2012; ROQUET et collab., 2013].

En conclusion et contrairement à ce qu'impliquait l'introduction, il n'y pas de raison de supposer que la similarité de niche climatique serait liée à la similarité phylogénétique à l'échelle phylogénétique de l'ensemble des Angiospermes et à l'échelle régionale des Alpes [THUILLER et collab., 2014] ou d'une vallée alpine (Chapitre 3).

Si on peut exclure la niche climatique comme origine d'un signal de similarité écologique dans la phylogénie d'où vient la forte diversité β phylogénétique des communautés de la Guisane (Chapitre 3) et des Alpes [THUILLER et collab., 2014] ? Cela est plus probablement dû aux diversifications des genres "alpins" [BOUCHER et collab., 2012; SCHWERY et collab., 2014]. La flore de haute altitude s'en trouve déséquilibrée avec ces genres qui contribuent de façon disproportionnée à sa richesse par rapport aux flores de basse altitude [OZENDA, 2002]. Le fait que les espèces de ces genres ont typiquement une abondance intermédiaire ou rare explique pourquoi le patron n'est observé que lorsque les indices de diversité ne prennent pas en compte l'abondance ce qui était la démarche des deux études. Plus d'études intégrant ces processus de spéciation (ex. PIGOT et ETIENNE [2015]) permettront probablement de préciser si cette hypothèse est correcte ou si cette forte diversité β est bien dû à un filtrage climatique.

En conjonction avec le patron de diversité prenant en compte l'abondance des espèces qui suggérait que des lignées récentes étaient dominantes dans l'ensemble de la Guisane, cela suggère qu'il y a une double relation entre similarité de niche climatique et dissimilarité phylogénétique dans la phylogénie de la flore des Alpes (Figure 6.2).

1. Des lignées spécialisées d'espèces localement peu abondantes qui sont similaires en terme de niche climatique. Cette similarité ne nécessite pas de supposer un sélection stabilisante de la niche climatique, qui en fait est plutôt labile [ARAÚJO et collab., 2013]. En fait, une radiation de ces espèces dans le milieu alpin suffit à générer un patron de forte similarité de niche climatique entre elles par rapport au reste de la flore des Alpes.

2. De l'autre coté, des lignées avec une niche climatique labile dont les espèces sont capables d'être dominantes sur une grande portion des gradients environnementaux comme c'est le cas de Pooideae qui à l'échelle biogéographique sont riches dans les zones montagneuses [VISSER et collab., 2014], ce qui tendrait à suggérer un partitionnement de la niche climatique le long des gradients au sein des ces lignées. La résolution des relations phylogénétiques au sein de ces genres dominants (la phylogénie utilisée n'est résolue qu'au genre) pourra éventuellement révéler la fameuse relation monotone décroissante dans l'hypothèse qu'il y ait un signal phylogénétique de la niche climatique. On peut supposer qu'alors la diversité β phylogénétique sera plus élevée qu'attendue à cause des gradients climatiques à petite échelle phylogénétique, c'est-à-dire au sein de ces lignées, et ce même pour des indices de diversité prenant en compte l'abondance (ex. JIN et collab. [2015]).

Niches au sein des écosystèmes herbacées

Si la phylogénie des Angiospermes contient le signal de la biogéographie à une large échelle phylogénétique et hypothétiquement un signal de la niche climatique à petite

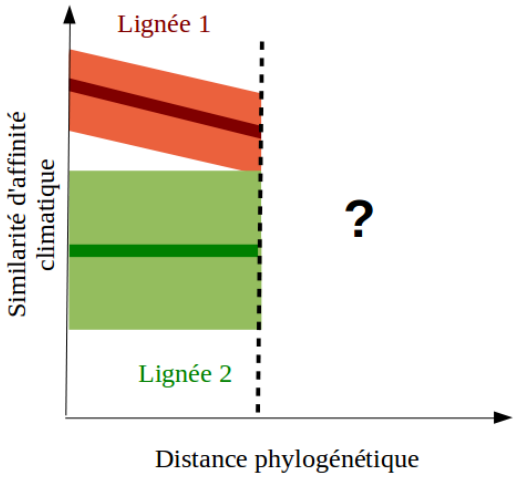

FIGURE 6.2 – Relation hypothétique entre similarité d'affinités climatiques et distances phylogénétiques telles qu'elle est suggérée par le Chapitre 2.1. La lignée 1 (rouge) représente les lignées rares filtrées par le climat et la lignée 2 (verte) représente les lignées dominantes sur l'ensemble du gradient. Les zones claires représentent l'intervalle de confiance de la relation des deux lignées. Le point d'interrogation représente l'incertitude dans le type de relation émergeant à plus large échelle phylogénétique.

échelle phylogénétique, y a t-il une quelconque similarité écologique contenue dans la phylogénie des Angiospermes des Alpes ?

Le travail du chapitre 3 montre qu'on trouve des patrons phylogénétiques non stochastiques à l'échelle des Angiospermes qui sont cohérents avec le principe d'un axe de similarité écologique liée à la similarité phylogénétique. Les résultat de cette étude suggère ainsi une diversité β phylogénétique plus faible qu'attendue, ce qui combinée avec le fait que les gradients environnementaux étaient important suggèrent une stabilité phylogénétique importante des communautés herbacées des Alpes. Nous avons interprété ça comme une conséquence de la compétition qui favorise la coexistence récurrente des mêmes lignées phylogénétiques (ex. Poales, Asteraceae, Fabaceae) dans les écosystèmes herbacées de Alpes sur une grande partie du gradient des conditions abiotiques. C'est une constatation également faite dans écosystèmes prairiaux non montagnards (ex. BERNARD-VERDIER et collab. [2013]). Les relations phylogénétiques entre espèces à l'échelle des Angiospermes semblent en fait davantage définir les grandes niches écologiques au sein des communautés associées aux principaux groupes fonctionnels herbacés [CORNWELL et collab., 2014; TILMAN et collab., 1997], ce qui peut expliquer les effets de complémentarité de niche liés à la diversité phylogénétique qui y ont été observés [CADOTTE et collab., 2008, 2012]. ainsi que le lien entre la phylogénie des plantes et leur niche trophique [DINNAGE et collab., 2012; PELLISSIER et collab., 2013].

Règles d'assemblage, diversité phylogénétique et échelle phylogénétique

Au final, par rapport au cadre d'analyse de CAVENDER-BARES et collab. [2009], la méta-communauté alpine donne une autre vision de la relation entre règles d'assemblage et échelle phylogénétique. Il paraît peu probable d'observer un impact des gradients climatiques à une échelle phylogénétique large en étudiant les méta-communautés des Alpes. Au contraire, il est plus probable qu'un tel patron s'observe davantage à une échelle phylogénétique fine. Ce que montre mon travail est que l'échelle phylogénétique des Angiospermes des Alpes témoigne davantage des interactions biotiques au sein des communautés en reflétant les principales lignées dominantes des méta-communautés alpines.

1.3 Conclusion

Le Chapitre 3 a montré que la diversité fonctionnelle et phylogénétique des communautés ne quantifie pas les mêmes caractéristiques écologiques et suggèrent des mécanismes d'assemblage différents. En fait, les différents travaux de ma thèse ont montré qu'il y a un lien étroit entre traits fonctionnels et gradients environnementaux à petite comme à grande échelle spatiale alors que la diversité phylogénétique semble peu connectée aux gradients environnementaux. Cela va dans le sens de la littérature qui montre que les diversités fonctionnelles et phylogénétiques des communautés herbacées sont faiblement corrélées [FLYNN et collab., 2011] et suggèrent des règles d'assemblage différentes [BERNARD-VERDIER et collab., 2013; CIANCIARUSO et collab., 2012]. Une façon de rassembler traits fonctionnels et phylogénie dans un ensemble cohérent sont les notions de niche α et β [ACKERLY et CORNWELL, 2007]. C'est-à-dire respectivement la niche écologique qu'occupe une espèce au sein d'une communauté et sa niche le long des gradient environnementaux. Dans cet ordre d'idée, les différents travaux de cette thèse suggèrent que la niche β est étroitement associée aux variations de traits fonctionnels et ne semble pas avoir de signal phylogénétique. En revanche, la niche α de la flore des Alpes semble elle présenter un signal phylogénétique. La question de savoir à partir de quels trait phénotypique cela se construit reste ouverte.

2 Multiplier les choix méthodologiques

2.1 Choisir... puis ne pas choisir un indice de diversité

Les nombres de Hill et leurs extensions phylogénétiques et fonctionnelles utilisées tout au long de cette thèse ne constituent qu'un petit nombre des métriques utilisées pour quantifier la diversité des communautés. Comme affirmé par de nombreux auteurs [PIELOU, 1975; RICOTTA, 2005], ce que recouvre le concept de "diversité" d'une communauté dépasse ce que peut décrire la statistique "indice de diversité" ce qu'atteste la multiplicité des indices [PAVOINE et BONSALL, 2011]. Une conséquence directe est que le choix

d'un indice de diversité est difficile à justifier par son habileté à quantifier la "diversité" comme le critiquait vertement HURLBERT [1971]. Ce qui peut justifier le choix d'un indice de diversité peut donc être la désirabilité de ses propriétés mathématiques [ROUTLEDGE, 1979], son efficacité face à des objectifs analytiques [RICOTTA, 2005] et la facilité de son interprétation [JOST, 2007]. Un autre critère qui me semble adéquat à l'issue de cette thèse est la généralité de l'indice de diversité et à quel point il permet au scientifique de faire le moins possible d'hypothèses de travail.

À ce titre, individuellement les nombres de HILL [1973] et leurs généralisations en indices de diversité fonctionnelle et phylogénétique [CHAO et collab., 2010; LEINSTER et COBBOLD, 2012], ne se distinguent pas particulièrement : ils restent des fonctions particulières, plutôt complexes qui ne se distinguent pas par un "réalisme biologique" particulier.

En revanche, ils présentent deux avantages. Le premier est la cohérence de leur décomposition. La standardisation numérique de la diversité β, toujours comprise entre 1 et le nombre de communautés à partir desquelles elle est estimée rend facilement comparable sa valeur entre des écosystèmes qui n'ont pas le même degré de diversité α [JOST, 2007]. Dans le chapitre 5, grâce à cette propriété, nous avons pu mettre en perspective l'hétérogénéité de communautés de lignées phylogénétiques qui ne fonctionnent pas sur la même échelle de diversité α et γ. La comparaison numérique des diversités β de ces systèmes a certes des limites parce qu'elle ne permet pas d'inférer des différences de processus écologiques qui nécessite toujours l'usage d'un modèle nul [CHASE et MYERS, 2011; KRAFT et collab., 2011]. En revanche, cela permet de pouvoir répondre à la question "quelle est la lignée dont les communautés changent le plus dans le paysage ?" sans qu'aient pu biaiser les différences d'échelle de diversité entre ces lignées (maximum de 4019 MOTUs par échantillon de bactéries contre 22 MOTUs pour les plantes). La décomposition des nombres de Hill se caractérise aussi par la souplesse notamment dans la décomposition entre niveaux hiérarchiques successifs [TUOMISTO, 2010], dans le chapitre 4, j'ai pu démontrer qu'elle possède des propriétés numériques similaires à la décomposition simple α, β, γ. Dans le chapitre 5, cela a permit de décomposer facilement la diversité dans une hiérarchie décrivant la structure spatiale de la zone d'étude entre paysage, site, communauté et échantillon et de quantifier tout les niveaux d'hétérogénéité tout en conservant les propriétés numériques de la décomposition simple entre composantes de diversité α, β, γ.

Le second avantage, illustré par les chapitres 3 et 5 est que le lien de l'indice avec la dominance et similarité entre espèces peuvent être explicitement paramétrés et interprétés (relativement) facilement en terme écologiques (dominance, rareté) ou évolutifs (hypothèse d'évolution ancienne ou récente de la niche, PAGEL [1999]). Le résultat d'une paramétrisation donnée peut être interprété directement par rapport aux hypothèses biologiques qu'elle implique et aux résultats obtenus par d'autres paramétrisations. Cela est facilité par les propriétés mathématiques communes qu'ont ces indices de diversité qui les rendent facilement comparables. Au final, ils constituent un cadre méthodologique

pratique autorisant au scientifique le luxe de ne pas choisir d'hypothèse de travail particulière et d'explorer à loisir la robustesse d'une conclusion écologique, ou, plus amusant, son absence de robustesse, afin d'obtenir une image plus complète du système étudié.

Une perspective méthodologique importante vis-à-vis des nombres de Hill est de préciser le lien entre profil de diversité et des patrons particuliers de distribution de l'abondance des espèces dans les sites d'une méta-communauté. SCHEFFER et VAN NES [2006] ont ainsi montré que la séparation de niche entre espèces en coexistence peut générer des distributions d'abondances difficilement classifiables selon la dichotomie convergence/divergence (Figure 6.3). Dans ce cas précis, on peut imaginer que l'utilisation de nombres de Hill prenant en compte la dissimilarité de niche, pourra détecter pour $q = 0$ que les espèces sont groupées le long de l'axe de niche (convergence de niche) mais qu'en même temps les espèces les plus abondantes (pour une valeur élevée de q) sont dispersées sur l'axe de niche (divergence de niche).

Il me paraît ainsi nécessaire de produire des grilles de lecture des profils de diversité α et β afin de rendre plus aisée l'interprétation de certains patrons complexes (ex. Chapitre 3 et 5) ainsi que leur lien avec les processus écologiques susceptibles de les produire. Étant donné qu'à l'heure actuelle le paradigme convergence/divergence au sein des communautés ne permet pas de distinguer l'éventail des processus écologiques capable de générer la diversité des communautés [MAYFIELD et LEVINE, 2010], il est possible que l'ajout de la dimension "q" permettra de faire des inférences patrons-processus plus précises.

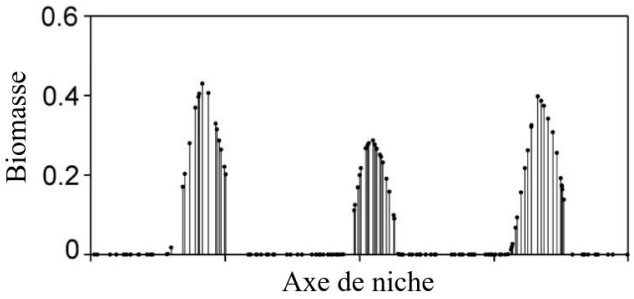

FIGURE 6.3 – Un patron complexe des abondances d'une communauté le long d'un axe de niche : la similarité "auto-organisée". Modifié de SCHEFFER et VAN NES [2006]

2.2 Le modèle nul et la perspective alpine

La base de l'analyse des patrons de diversité par l'utilisation d'un modèle nul est de considérer qu'il y a une possibilité qu'une structuration observée dans la communauté soit due au hasard. Conceptuellement, cela s'approche de la théorie neutre de Hubbell qui montrait que l'émergence de structure dans l'assemblage peut être due seulement à la stochasticité. Or l'emploi simple d'un modèle nul pour tester si l'assemblage d'une méta-communauté alpine est stochastique, permet typiquement de "découvrir" que ce

n'est pas le cas et que la végétation alpine est structurée par les grands gradients environnementaux. Comme illustré auparavant, ce sont des conclusions importantes qui permettent de mieux comprendre l'adaptation des communautés alpines à des conditions de stress [DE BELLO et collab., 2013] et reste un travail majeur à réaliser pour améliorer notre compréhension des communautés alpines ainsi que leur modélisation [BOULANGEAT et collab., 2014].

Cela étant dit, la conclusion que l'assemblage des communautés alpines n'est pas stochastique mais est contrainte par des gradients abiotiques à large échelle enfonce des portes ouvertes, il s'agit après tout d'une des plus anciens résultats de l'écologie scientifique [VON HUMBOLDT, 1807]. Pour peu qu'une méta-communauté alpine soit située sur une grande étendue spatiale, on s'attend fortement à observer un patron non aléatoire de diversité determiné par les grands gradients de stress. En fait, ce serait davantage une surprise de constater qu'une caractéristique quelconque du patron de diversité ne le soit pas.

Mes travaux ne dérogent pas à cette règle. Ainsi dans le chapitre 1, l'approche classique avec un modèle nul à large étendue spatiale révélait que les communautés étaient souvent fonctionnellement convergentes. Dans le chapitre 2, tout les traits moyens de communautés variaient individuellement dans leur moyenne en réponse au gradient de stress climatique et la diversité fonctionnelle des communautés étaient affectée (1) par le passage d'une étendue spatiale représentant le paysage à une étendue spatiale représentant des conditions climatiques homogènes et (2) variait le long du gradient climatique. Enfin, dans la partie 3 et d'après le travail de THUILLER et collab. [2014], la diversité β fonctionnelle et dans une moindre mesure phylogénétique présentaient tout deux l'empreinte d'un filtre abiotique important.

À mon sens, l'évidence du filtre abiotique offre une perspective différente sur la méthodologie classique de l'étude de l'assemblage des communautés, en particulier des modèles nuls. À la base, un modèle nul cherche à reproduire un patron observé via un mécanisme stochastique [GOTELLI et GRAVES, 1996] ; l'hypothèse nulle formulée est alors "les communautés sont des échantillons aléatoire du pool d'espèces régional" avec quelques variations selon les contraintes du du modèle nul [HARDY, 2008]. Très rapidement, sur les communautés végétales alpines, il paraît plus pertinent de se poser les questions suivantes : "au-delà du filtre climatique, y a t-il un assemblage stochastique des communautés ?" ou "certaines caractéristiques des plantes ne sont-elles pas filtrées par l'environnement (ex. la diversité phylogénétique, Chapitre 3) » ou « certaines caractéristiques sont-elles filtrées par autre chose que le filtre abiotique ? ». Cela revient en fait à reformuler l'hypothèse nulle : "les communautés sont uniquement le résultat du filtrage par les grands gradients climatiques ».

Reconstruire l'écologie des communautés à partir de pools d'espèces locaux

VELLEND et collab. [2014] recommandait d'intégrer davantage de données externes

aux modèles nuls, notamment environnementales, pour identifier avec plus de précision la composante stochastique des communautés et l'influence de processus déterministes qui leur sont subordonnées (interactions biotiques...). Les modèles nuls employés au cours de cette thèse suivent cette ligne de pensée, qu'ils soient basés sur des données de préférences climatiques des espèces comme le "suitability-based null model" (SB-R, Chapitre 1) ou sur les effets d'échelles comme le "site null model" (Chapitre 2), tentent de répondre à cette problématique du filtre abiotique en prenant pour acquis certaines caractéristiques du système, c'est-à-dire les conditions climatiques dans le premier et les filtres abiotiques à large échelle pour le second.

Ces deux modèles ont grossièrement le même but, c'est à dire de modéliser le pool d'espèces local et de tester si l'assemblage des communautés au sein de ces pools est aléatoire. Ils incluent cependant un ensemble d'hypothèses différentes, SB-R est uniquement basé sur la modélisation des préférences climatiques des espèces, à ce titre, il ne prend ni en compte que les traits des espèces alpines varient le long des gradients climatiques [ALBERT et collab., 2010b] mais aussi le fait que certaines espèces puissent être absentes du pool d'espèces local à cause de la limitation de la dispersion ou des effets de priorité [FUKAMI et collab., 2005].

Le second modèle nul est plus strict et est en quelque sorte le "pool d'espèces réalisé" il n'inclut que les espèces effectivement trouvées localement et parce qu'il était couplé avec un échantillonnage local des traits, il inclut l'effet des gradients climatique sur la variabiltié intraspécifique. En revanche, par rapport au premier, il exclut la détection de la diversité "sombre" [PÄRTEL et collab., 2011] car l'exclusion locale de ces espèces par d'autres facteurs que le climat est actée par le modèle. Ces deux modèles nuls viennent compléter des modèles déjà existants tel que le modèle nul basé sur le pool fonctionnel [DE BELLO et collab., 2012] qui se base sur les préférences d'habitat des espèces. Au final ces trois modèles nuls représentent une hiérarchie dans le grain spatial du pool d'espèces local avec le modèle de DE BELLO et collab. [2012] en position intermédiaire.

L'usage de ces modèles nuls a permis d'identifier une composante stochastique dans l'assemblage local des communautés dans le chapitre 1 (dans la mesure où l'approche par modèle nul est capable de le faire, VELLEND et collab. [2014]). Dans le chapitre 2, le modèle nul "site" nous a permis d'identifier des processus locaux (cf. Section 1.1). Ces conclusions sont importantes dans le sens où elles permettent de faire le lien avec les études à petite échelle spatiale qui ont été réalisés sur les communautés subalpines et alpines [CHOLER, 2005; GROSS et collab., 2009; POTTIER et collab., 2007].

En revanche, on ignorait si ces processus sont suffisamment importants pour laisser une empreinte dans le patron de diversité des communautés ou s'ils ne sont que des épiphénomènes à négliger [RICKLEFS, 2008]. En fait, il a été montré que prédire la composition des communautés alpines en empilant les prédictions de présence de chaque espèce étudiée, POTTIER et collab. [2013] conduisait à une surévaluation de la diversité des communautés mettant ainsi en valeur le problème de la non prise en compte les pro-

cessus sous-jacents au climat se produisant à petite échelle spatiale [ELITH et LEATHWICK, 2009]. Le corollaire d'un tel problème est que cela oblige à dégrader la résolution du modèle de distribution des communautés (ex. THUILLER et collab. [2014]), où la prédiction de la diversité se fait à une résolution de 2.5km contre une résolution initiale de 250 m) ce qui montre que ce type de modèle semble à l'heure actuelle plus adéquat pour prédire la composition des pools d'espèces locaux plutôt que des communautés. Déplacer le cadre d'analyse des patrons de diversité en étudiant davantage comment les communautés s'assemblent à partir des pools locaux plutôt qu'à partir de pools régionaux pourra peut-être permettre de mieux définir les règles d'assemblage locales telle que les interactions biotiques mais aussi les effets de la dispersion et des contingences historiques qui ont été ignorées dans cette thèse [FUKAMI et collab., 2005; VELLEND et collab., 2014]. La prise en compte de ces processus locaux et de leur répercussion à large échelle spatiale pourra se révéler être un atout majeur pour l'amélioration de la prédiction de la diversité des communautés et donc de ses applications en conservation.

3 Vers des approches plus intégrées ?

L'étude des patrons de diversités des communautés part d'une question simple : "est-ce que la diversité d'une communauté est un échantillon aléatoire des espèces présente dans la région ?" et se traduit en règle générale par une analyse simple comparant un ou deux indices avec un unique modèle nul (ex. WEBB et collab. [2002]). Or les communautés sont des entités complexes et leur structure est déterminées par un grand nombre de processus qu'une telle démarche n'est pas capable de détecter. Les différents travaux de cette thèse dessinent la valeur de méthodologies plus intégrées pour étudier les patrons de diversité. Les axes d'intégration peuvent se faire via l'utilisation de plusieurs modèles nuls intégrant d'autres sources d'informations que la distribution des espèces dans les communautés étudiées (ex. climat, Chapitre 1 ; processus évolutifs, PIGOT et ETIENNE [2015]), de différents indices de diversité (Chapitre 3), de plusieurs sources de données de similarité (Chapitre 1, 3, THUILLER et collab. [2014]). Tout ces éléments permettent la découverte de règles d'assemblage particulières qui auraient été ratées si l'exploration des différentes possibilités méthodologique avait été négligée. C'est une approche qui n'est pas sans défaut. Elle est complexe car si théoriquement, on peut étudier un unique jeu de données en faisant varier toutes ces dimensions à la fois ; dans les faits cela provoque la gestion d'une quantité de résultats difficilement exploitable. Dans ce cadre, l'écologie in silico peut amener des perspectives intéressantes pour tester à priori l'efficacité de ces méthodes sur des communautés dont l'assemblage obéi à des règles simples et connus à l'avance [GALLIEN et collab., 2014; MÜNKEMÜLLER et collab., 2012].

Les communautés sont des entités complexes structurées par un grand nombre de processus écologiques qui diffèrent selon l'écosystème étudié. Cela a pu amener des auteurs à critiquer la pertinence de l'échelle des communautés pour comprendre les méca-

nismes qui structurent la diversité [LAWTON, 1999; RICKLEFS, 2008]. En fait, il est possible que cette apparente absence de “lois générales” soit en fait dû à la simplicité des méthodes utilisée par rapport à la complexité de la communauté. Relever le défi de caractériser des patrons plus complexes par le biais de méthodologies plus intégrées amène des perspectives passionnantes pour identifier les lois générales de l’assemblage des communautés et pour distinguer les modalités avec lesquelles elles peuvent s’appliquer à des écosystèmes très différents.

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Annexe A

Articles en tant que co-auteur

1 A global meta-analysis of the relative extent of intraspecific trait variation in plant communities

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Abstract

Recent studies have shown that accounting for intraspecific trait variation (ITV) may help better address major questions in community ecology. However, a general picture of the relative extent of ITV compared to interspecific trait variation in plant communities is still missing. Here, we conducted a meta-analysis of the relative extent of ITV within and among plant communities worldwide, using a database encompassing 629 communities and 36 functional traits. Overall, the contribution of ITV to total within- and among-community trait variance was 30-40% that of interspecific variation on average. The relative extent of ITV tended to be greatest for traits related to plant size and leaf economics, and for communities sampled at fine spatial scales and with low species richness. These results highlight global patterns in the relative importance of ITV in plant communities, providing practical guidelines for when researchers should include ITV in trait-based community and ecosystem studies.

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Are different facets of plant diversity well protected against climate and land cover changes? A test study in the French Alps

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Climate and land cover changes are important drivers of the plant species distributions and diversity patterns in mountainous regions. Although the need for a multifaceted view of diversity based on taxonomic, functional and phylogenetic dimensions is now commonly recognized, there are no complete risk assessments concerning their expected changes. In this paper, we used a range of species distribution models in an ensemble-forecasting framework together with regional climate and land cover projections by 2080 to analyze the potential threat for more than 2500 plant species at high resolution (2.5×2.5 km) in the French Alps. We also decomposed taxonomic, functional and phylogenetic diversity facets into α and β components and analyzed their expected changes by 2080. Overall, plant species threats from climate and land cover changes in the French Alps were expected to vary depending on the species' preferred altitudinal vegetation zone, rarity, and conservation status. Indeed, rare species and species of conservation concern were the ones projected to experience less severe change, and also the ones being the most efficiently preserved by the current network of protected areas. Conversely, the three facets of plant diversity were also projected to experience drastic spatial re-shuffling by 2080. In general, the mean α-diversity of the three facets was projected to increase to the detriment of regional β-diversity, although the latter was projected to remain high at the montane-alpine transition zones. Our results show that, due to a high-altitude distribution, the current protection network is efficient for rare species, and species predicted to migrate upward. Although our modeling framework may not capture all possible mechanisms of species range shifts, our work illustrates that a comprehensive risk assessment on an entire floristic region combined with functional and phylogenetic information can help delimitate future scenarios of biodiversity and better design its protection.

Changes in climate, notably a warming climate, are expected to strongly impact biodiversity in mountain environments (Pauli et al. 2012). Species are expected to migrate upward to keep pace with suitable climates, which should lead to an increase of diversity in higher altitudes in the near term (Walther et al. 2005). In return, it should ultimately lead to a decline in the number of species specialized for high alpine conditions, outcompeted by more competitive species from low-lands (Pauli et al. 2012). Earlier modeling studies that projected and analyzed future trends in mountain floras have shown dramatic decline of alpine species and strong spatial turnover (Thuiller et al. 2005). However, those studies carried out at European scales and coarse spatial resolution were not able to correctly account for mountain peculiarities such as topographic micro-heterogeneity and meso-scale refuges (Randin et al. 2009, Carlson et al. 2013). Recent studies have instead shown that when models were applied to high resolution, specifically over mountains, results were less pessimistic, indicating that mountain floras could still persist in some specific areas (Engler et al. 2011, Dullinger et al. 2012).

In addition to the threat from an altering climate, land cover is expected to change in the coming century in response to both, climate and socio-economic changes, the latter driven by demographic growth and changes in agricultural practices. Although land cover change is known to be one of the strongest drivers of biodiversity change (Sala et al. 2000), most risk assessments have only considered climate change (but see Barbet-Massin et al. 2012). The combination of both climate and land cover changes could however favor some particular species to the detriment of others. For instance, extension of forest cover due to land abandonment and an increased demand in wood products is an important driver of change in sub-alpine ecosystems. To date, no risk assessment has been carried out to evaluate the dual effects of climate and land cover change on the entire flora of a biogeographic region like the French Alps.

In addition to climate and land cover change threats to species ranges, it is also important to forecast the dual effects of these changes on the various facets of biodiversity. Despite few exceptions (Thuiller et al. 2011, Buisson et al. 2013), most of published biodiversity scenarios so far have only considered species richness and taxonomic turnover and their future protection status over a continent (Araújo et al. 2011). Although it is obviously of interest to examine the consequences of climate and land cover changes on species richness, this approach implies that all species are independent phylogenetic and functional units. An alternative view is to account for the shared evolutionary history of species and assess how phylogenetic diversity might be influenced by environmental change (Thuiller et al. 2011, Faith and Richards 2012). In addition, such a complementary view also considers that species share more or less similar functions based on their trait values (Violle et al. 2007) and that environmental change affects the distribution of trait diversity across space and time in a different manner than sole species richness (Thuiller et al. 2006, Buisson et al. 2013). The spatial patterns of these other facets of biodiversity are increasingly investigated at global (Safi et al. 2011) and regional scales (Devictor et al. 2010, Pio et al. 2011), but no study has investigated, so far, the projected re-arrangement of different biodiversity facets in response to environmental change in a region for a complete group of species such as plants. In a mountain environment such as the French Alps, we expect higher spatial variation in taxonomic diversity than in both functional and phylogenetic diversity since several species belong to the same functional groups or lineages. More particularly, we expect that in extreme environments (e.g. cold temperature), the current functional diversity will likely increase in response to climate warming due to the upward migration of lowland species. Concerning phylogenetic diversity, we expect to see less spatial variation of phylogenetic diversity than species or functional diversity under both current and future conditions since few large lineages dominate the entire region. Spatial re-shuffling of species within those lineages should not drastically change this pattern. This obviously represents a contrast between taxonomic, functional and phylogenetic diversity that leads to important patterns of changes. An additional advantage of looking at different facets of biodiversity in response to environmental change is the possibility to decompose diversity into spatial components, namely α, β and γ diversity. This allows measuring whether environmental changes result in local changes (α-diversity) or rather influence the spatial turnover between sites (β-diversity). Conservation actions to protect species and diversity should ultimately account for those different facets, but there exist only few studies looking at whether the current protected area networks are able to jointly protect species and biodiversity facets in the context of expected environmental changes.

In this paper, we take these challenges by assessing the response of the entire flora of the French Alps at high spatial resolution (i.e. 250 m) to both regional climate and land cover changes. We address here three main questions: 1) what are the potential consequences of climate and land cover changes on plant species distributions and associated trait characteristics in the French Alps? 2) Will the spatial re-arrangement of species influence the spatial distribution of taxonomic, phylogenetic and functional diversity patterns? 3) Is the current protected area network sufficient to protect both threatened species and the different facets of biodiversity in a warmer world? To address these questions, we modeled the spatial distribution of the whole flora of the French Alps at high resolution using bedrock, climate and land cover variables in an ensemble-forecasting framework (Araújo and New 2007). Using downscaled regional climate models and a range of land cover change scenarios, we then investigated whether plant species would likely loose or gain suitable environmental space. We tested whether differential responses occurred between rare and common species, life forms or IUCN species threat categories. At the assemblage level, we then used a framework based on Hill's numbers (Hill 1973, Chao et al. 2010) that allowed us to decompose α-diversity and β-diversity into meaningful numbers (i.e. equivalent number, Jost et al. 2010) for taxonomic, phylogenetic and functional diversity (Leinster and Cobbold 2012). We finally built an innovative gap analysis to measure the ability of the current protected area network to protect both species and the different facets of biodiversity for the horizon 2080.

Material and methods

Study area

This study was conducted over the French Alps region (Fig. 1), which covers 26 000 km^2 and presents a wide range of environmental conditions due to mixed continental, oceanic and Mediterranean climate influences and steep altitudinal gradients.

We used a vegetation database from the National Alpine Botanical Conservatory (CBNA, Fig. 1, dark grey shading in the national map), including more than 164 500 sampling plots recorded between 1980 and the present at a resolution greater than or equal to 250 m. Two sampling methods were used: 31 569 of these plots corresponded to comprehensive phytosociological relevés (i.e. phytosociological method hereafter) and thus provided both presence and absence data, whereas the rest of the plots consist of presence-only data (i.e. single occurrence method hereafter). We started with the 3250 plant species present in the CBNA database, based on a standardized species taxonomic nomenclature (Kergélen 1993).

To complement these data, we also gathered additional 4000 occurrence data points from the National Mediterranean Botanical Conservatory (CBMED) for 1000 species from the previous list that also occur in the extreme south of French Alps (Fig. 1, light grey shading in the national map). This additional information from the Mediterranean area allowed us to be confident that the warm portion of species niches was adequately captured (Fig. 1). All presence and absence information were overlaid to the 250 m analysis grid. When at least one presence was recorded for a given species over a 250 m pixel, it was noted as presence. This procedure has the advantage of smoothing the sampling bias in highly sampled sub-regions.

We then removed species occurring in less than 20 pixels to make sure enough information was provided to the models

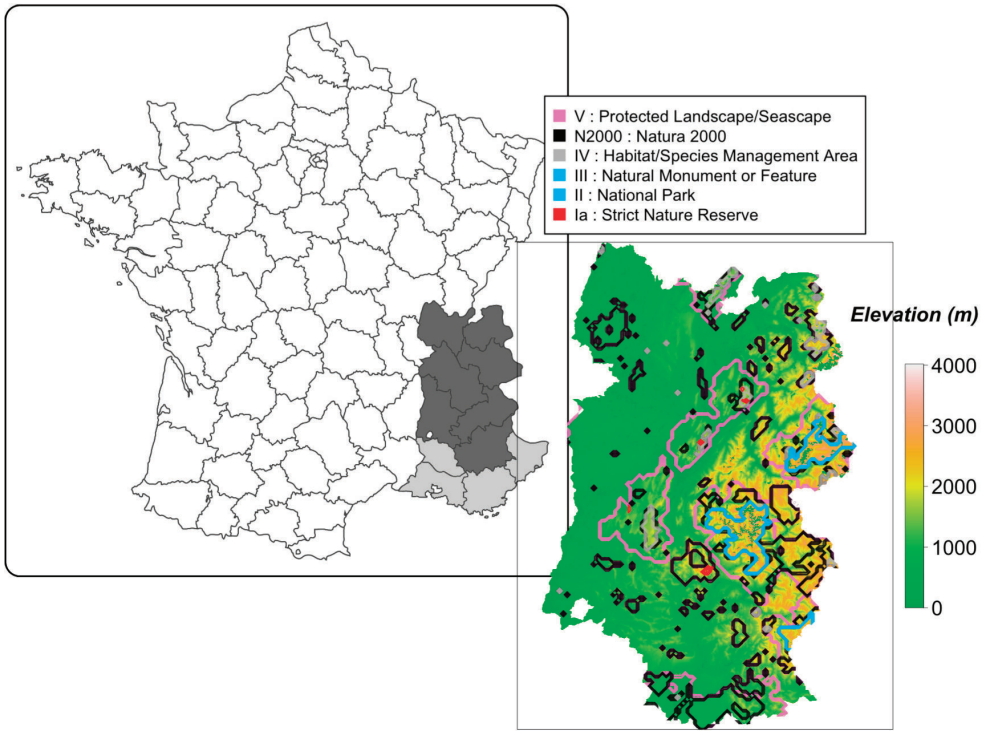

Figure 1. Representation of the study area. Dark grey shades represent the study area where the risk assessment was conducted (CBNA zone). Light grey shades represent the area where additional presence–absence information was gathered for calibrating the models (CBNMED zone). The zoom represents the current protected area network in the French Alps (CBNA zone) with the different labeling corresponding to the official classification (WDPA 2005).

for fitting meaningful relationships. We thus retained 2857 species for our modelling analysis over the French Alps.

Chorological information

Rarity classification – we used a measure of regional rarity that classifies the species from our study area based on a protocol from the CBNA (Supplementary material Appendix 2, Table A1). It is based on the 250 m analysis grid we used for our study area. $R = 100 - [100 \times T/C]$, where C is the total number of 250 m pixels in the study area and T is the number of 250 m pixels where the species was recorded as present.

Red list classification – in order to classify the threat status of all plant species of the region, we used the National and Regional Red Lists. When a species was present in the national red list I, it was considered as 'priority species'; when present in the national list II, it was considered as 'strictly protected'; and finally, when a species was only present in the regional list of the French Alps, it was considered 'locally protected'. Remaining species were classified as 'unprotected'.

Each of our study species was further classified into altitudinal vegetation life zones. To do so, we followed Engler et al.'s (2011) approach by dividing our study area into four vegetation belts (Theurillat 1991). Alpine: life zone with a vegetation period lasting ~50–100 d yr^{-1} (i.e. mean annual temperature < 3°C) and encompassing exclusively vegetation above the upper limit of the natural treeline. Only grasslands or low shrublands dominated by low chamephytes such as dwarf *Salix* sp. are found in this vegetation belt. Subalpine: life zone with a vegetation period lasting ~100–200 d yr^{-1} (i.e. mean annual temperature between 3 and 6°C) and located between the closed montane forest and the uppermost limit of small individuals of tree species. This zone represents the transition zone between fully-grown forest and Alpine grasslands. Deciduous trees are mostly absent from this vegetation belt, which is dominated by conifers. Montane: life zone with a vegetation period of ~200–250 d yr^{-1} (i.e. mean annual temperature between 6 and 10°C) where the native vegetation is mainly composed of fully grown coniferous forest, or mixed forests with deciduous trees such as *Fagus sylvatica*. Colline: lowest and warmest life zone with a vegetation period of more than 250 d yr^{-1} (i.e. mean annual temperature > 10°C) and where the native vegetation is mainly composed of deciduous tree species such as *Quercus* sp., *Fraxinus* sp. or *Acer* sp.

Trait information

For the functional diversity analyses, we focused on three key functional traits: the specific leaf area (SLA, light-capturing area deployed per unit of leaf dry mass), the height of plant's canopy at maturity and the seed mass, that are well known components of the leaf-height-seed (LHS) syndrome of plant traits (Westoby 1998). Seed mass relates to dispersal distance and establishment success, height is considered as a surrogate of species' ability to intercept light, while SLA strongly relates to species relative growth rate (Westoby et al. 2002). In addition, we added life form information to reflect integrated strategies and longevity. All trait diversity analyses

were conducted with these four traits that we log-transformed (for SLA, height and seed mass) prior to the analyses.

These traits were extracted from the trait database ANDROSACE (Thuiller et al. unpubl.). The database includes trait information for Alpine plants from individual projects and freely available databases such as LEDA (Knevel et al. 2003), BioFlor (Kühn et al. 2004), Ecoflora (Fitter and Peat 1994) and CATMINAT (Julve 1998). We excluded 102 species for which we had less than two traits for the LHS syndrome, which left us with 2755 species for analyses.

Phylogenetic information

We reconstructed a genus-level phylogeny based on DNA sequences available in GenBank, using the procedure proposed in Roquet et al. (2013). We used the following DNA regions: three conserved chloroplastic regions (rbcL, matK and ndhf) and 8 regions for certain families or orders (atpB, ITS, psbA-trnH, rpl16, rps4, rps4-trnS, rps16, trnL-F). Global or taxonomically local alignments were performed with several algorithms (implemented in MAFFT, (Katoh et al. 2002); MUSCLE, (Edgar 2004); and Kalign, (Lassmann and Sonnhammer 2005) and then compared with the program MUMSA to select the best alignment (Lassmann and Sonnhammer 2005). Alignments were then cleaned with TrimAl (Capella-Gutierrez et al. 2009) to remove ambiguously aligned regions before performing a phylogenetic inference analysis with RAxML (Stamatakis 2006). The phylogenetic inference was performed while constraining deep nodes based on a family level angiosperm supertree (based on Davies et al. 2004, Moore et al. 2010). We extracted from the phylogenetic inference a set of 100 trees closes to the maximum likelihood score. Because there was little difference in topology and likelihood between those trees and the best one (i.e. the tree with the highest log-likelihood), all subsequent analyses were only conducted with the best ML tree. This tree was dated using penalized likelihood as implemented in r8s (Sanderson and Driskell 2003) with 25 fossil constraints (extracted from Schuettpelz and Pryer 2009, Smith et al. 2009, Bell et al. 2010). Finally, we randomly resolved terminal polytomies by applying a birth-death (Yule) bifurcation process within each genus. We only used one randomly resolved tree here, while ideally, it should have been done 100 times. The main issue was that the overall analysis was impossible to run over 100 trees due to computational limitations. Using a similar approach for Europe plants, Thuiller et al. (2011) showed that the general patterns of phylogenetic diversity over Europe were relatively stable with respect to random resolution of polytomies.

Environmental data

We used a set of environmental variables that are known to be strong drivers of plant species distribution over the French Alps.

Variables included a soil map representing the percentage of carbon in the bedrock, derived from the harmonized geological map of the Alps (Bd-Charm 50 – BRGM; <www.geocatalogue.fr/Detail.do?id = 4156#>).

Current climate was mapped as a 250 m raster, downscaled from 1 km Worldclim climate grids (Hijmans et al. 2005). We first downscaled the monthly climate normals (1950–2000) to a spatial resolution of 250 m, to better represent the topographic variation of climate in our study area using a mowing window regression approach. In a second step we used these downscaled temperature and precipitation grids to derive maps of five bioclimatic variables, which 1) have an obvious impact on plant life in mountain environments; and 2) showed some independent variation across the study area ($r < 0.75$): isothermality (mean diurnal range/temperature annual range; bio3), temperature seasonality (bio4), temperature annual range (bio7), mean temperature of coldest quarter (bio11) and annual sum of precipitations (bio12). We refer to Dullinger et al. (2012) and its supplementary materials for more details on the downscaling procedure.

Future climate by 2050 and 2080 (2021–2050 and 2051–2080) was represented by a set of regional climate model (RCM) runs driven by two emission scenarios (A1B and A2), originating from the ENSEMBLES EU project, which has physically downscaled global circulation model (GCM) data generated for the 4th assessment report of the IPCC (2007). All RCM scenarios were statistically downscaled to the same 250 m spatial resolution using the change factor method (Anandhi et al. 2011). To further check the sensitivity of our results to RCM calculations, we have used 3 different RCMs, namely HadRM3, RCA3 and CLM (Jones et al. 2004a, b, Collins et al. 2006, Meijgaard et al. 2008) fed by three different GCMs (HadCM3, CCSM3 and ECHAM5, respectively) resulting in 3RCM/GCM combinations. We only made these estimates for A1B while for A2 we considered the combination RCA3 × CCSM3. The output from the three RCMs differ in the degree of projected warming by 2100, with the HadRM3, the CLM and RCA3 models generating average summer temperatures increases around 5.0°C, 3.8°C and 2.3°C, respectively. The relative changes in summer precipitation projected by 2100 by the RCMs HadRM3, CLM, and RCA3 amount to –10, –12 and –15%, respectively. This variability in projected climate trends for the A1B scenario represents well the variability assembled by the whole suite of model projections generated in the EU project ENSEMBLES.

Current land cover for the whole French Alps was represented by CORINE Land cover 2006 at 250 m resolution by using the level 1 classification (i.e. built-up areas, arable lands, permanent crops, grasslands, forests and others). However, to tease apart the effects of glacier and sparsely vegetated areas, we re-classified the class 'other' class into 7 classes (glacier, water, saline waters, bare rocks, sclerophyllous vegetation, sparsely vegetated areas, wetlands and others, by assigning level 2 classification values here) leading to a total of 12 classes.

Future land cover at 250 m was taken from the EU projects ALARM and ECOCHANGE (Dendoncker et al. 2006, 2008, Rounsevell et al. 2006) that we re-classified to meet the 12 classes of the current land cover maps, spanning the period 2006–2080. We then retained the period 2021–2050 and 2051–2080 to be consistent with the climatic data. We used two socio-economic storylines that are consistent with the climate change scenarios.

GRAS – growth applied strategy: deregulation, free trade, growth and globalisation will be policy objectives actively pursued by governments in this storyline. Environmental policies will focus on damage repair and limited prevention based on cost benefit-calculations. This scenario is considered equivalent to A1b. BAMBU – business-as-might-be-usual: policy decisions already made in the EU are implemented and enforced in this storyline. At the national level, deregulation and privatization continue except in 'strategic areas'. Internationally, there is free trade. Environmental policy is perceived as another technological challenge. This scenario is considered equivalent to A2.

We further used maps representing the current protected area network, which we extracted from the World Database on Protected areas (IUCN and UNEP 2009). It distinguishes seven categories ranging from 'strict natural reserve' (Ia) to 'protected area with sustainable use of natural resources' (VI) (Fig. 1). The category of Natura 2000 (N2000), which is not available within the IUCN framework, was additionally downloaded from the European environment agency (<www.eea.europa.eu/data-and-maps/data/natura-2000-eunis-database>). We then calculated zonal statistics using these two datasets to estimate the percentage of each 250 m cell of the study area covered by the N2000 and the seven IUCN categories.

Species distribution modeling

An ensemble of forecasts of species distributions models (SDM, Thuiller 2004, Araújo and New 2007, Marmion et al. 2009) was obtained for each of the 2755 species considered. The ensemble included projections from five statistical models, namely generalised linear models (GLM), generalised additive models (GAM), boosted regression trees (BRT), mixture discriminant analysis (MDA) and Random Forest (RF). Models were calibrated for the baseline period using a 70% random sample of the initial data and evaluated against the remaining 30% data, using both the area under the curve (ROC, Swets 1988), and the true skill statistic (TSS, Allouche et al. 2006). This analysis was repeated 2 times, thus providing a 2-fold internal cross validation of the models. All calibrated models were then projected under current and future conditions at a 250 m resolution over the whole French Alps (CBNA delimitation, Fig. 1). To summarise all projections into a meaningful integrated projection per species we used the weighted mean probability procedure, which gives the sum of all projections from all models and cross-validations weighted by their respective predictive performance estimated using the TSS (Marmion et al. 2009). However, we only included the models that reached both a TSS and ROC >0.3 and >0.8, respectively. The ensemble forecast was transformed into binary presence–absence maps using the threshold that maximises TSS. Models were calibrated from data from both CBNA and CBNMED regions (dark and light grey shading in Fig. 1) and were projected onto the CBNA region (French Alps) only (Fig. 1; dark grey shading). Models and the ensemble forecasting procedure were performed within the BIOMOD package (Thuiller 2003, Thuiller et al. 2009) in R.

Optimizing the spatial resolution of the analysis to get meaningful estimates of diversity metrics

One principal critique towards a SDM is that it neither accounts for dispersal limitation nor for biotic interactions (Elith and Leathwick 2009, Carlson et al. 2013). In other words, when single SDMs are stacked together for estimates of species richness or associated diversity metrics, they likely overestimate the observed diversity (Pottier et al. 2013). By assumption that dispersal and biotic interactions do influence the observed species richness and diversity at a finer resolution than does environmental filtering (Boulangeat et al. 2012), we therefore expect that stacked SDMs provide more meaningful predictions of species diversity when aggregating the data at lower resolution (i.e. reducing the pervasive effects of dispersal, biotic interactions and stochastic processes). We thus tested at which resolution our stacked SDMs were most accurate at predicting the observed species diversity starting from the original resolution at which species were modeled (250 m) to lower resolutions. To do so, we aggregated all modeled presence–absence species distribution under current conditions at different incremental spatial resolutions ranging from the original 250 m to 5 km. We did the same with the observed data. For both modeled and observed distributions, we considered a species present in one larger pixel when there was at least one presence at the consecutive higher resolution. We then compared the observed species richness with the projected one (stacked SDMs) across the whole French Alps at varying resolutions using Spearman rank correlations (Supplementary material Appendix 2, Fig. A1). We accounted for bias in sampling effort and the two sampling methods (see details in Supplementary material Appendix 1).

As expected, the correlation increased with coarser resolution. We selected the 2.5 km resolution as the best trade-off between high-resolution projections and appropriateness of the biodiversity estimates (Supplementary material Appendix 2, Fig. A1). All subsequent results and analyses have been performed at the 2.5×2.5 km resolution.

Measures of species' sensitivity

Each ensemble of binary species projections under current and future conditions was converted into two metrics of species' sensitivity.

The first metric gives the relative change in habitat suitability (CHS, or species range change) by measuring to what degree the future suitable area is larger or smaller than the current suitable area:

$$\text{CHS} = ([\text{Future suitable area} - \text{Current suitable area}]/\text{Current suitable area}) \times 100 \quad (1)$$

The second metric quantifies the proportion of the current range that will become unsuitable under future conditions, namely loss of suitable habitat:

$$\text{LSH} = 100 - [(\text{Overlap}(\text{Future},\text{Current})/\text{Current}) \times 100] \quad (2)$$

This metric allows to measure the risk of local extinction as it does not consider dispersal into new areas. A species losing

100% of its current suitable habitats is at high risk of extinction even if it is projected to gain new suitable habitats.

Diversity decomposition

The last few years have seen an upsurge of diversity metrics that can be used for measuring taxonomic, phylogenetic and trait diversity in a consistent way (Pavoine and Bonsall 2011, Tucker and Cadotte 2013). Here we used Leinster and Cobbold's (2012) framework that builds on a generalization of Hill's numbers (Hill 1973) to compute diversity metrics incorporating species differences (such as phylogenetic divergence of functional dissimilarity).

We used this framework to estimate both α and β-diversity for three biodiversity facets, namely taxonomic, phylogenetic and functional diversity under current and future conditions. α-diversity was estimated as the local diversity within each pixel for each of the three facets (following Eq. 3). The spatial turnover, β-diversity, was estimated using a moving window around each focal pixel. This moving window consisted of the 8 pixels contiguous to the focal pixel. γ-diversity was the total diversity of this window. The γ, α and resulting β components were then estimated for this window. The β value was then reported to the focal pixel and mapped. The general formula calculates the diversity D for a relative abundance vector p = {pi} of the S species present in the pixel, and a matrix Z containing the similarities Z_{ij} between species *i* and *j*:

$$D(p) = \left(\sum_{i=1}^{S} p_i \left(\sum_{i=1}^{S} z_{ij} p_j \right) \right) \quad (3)$$

The α-diversity of each pixel was calculated from the vector of species presences–absences per pixel, while the γ-diversity was calculated per window from the vector of species mean probability of presence over the moving 3 × 3 pixel window. The number of pixels to calculate β-diversity was chosen to ensure enough variability while keeping the setting around the focal pixel homogenous enough to be meaningful in term of species assemblages and meta-community structure (here 2.5 square kilometers).

The mean α-diversity of a window $\bar{\alpha}$ was calculated as the mean of the diversities of its constituent N = 9 pixels of α-diversity (inline) (Tuomisto 2010a, b). Finally the β-diversity of the window was calculated as the ratio of the γ-diversity and the mean α-diversity of a window. Z, the similarity matrix, was calculated as 1 minus the cophenetic distance between species for phylogenetic diversity and the Gower distance for the four selected traits (SLA, height, seed mass and life form) for trait diversity, divided by the maximum respective distance to have Z bounded by 0 and 1.

The advantage of using a multiplicative framework of α, β, and γ decomposition with Leinster and Cobbold's (2012) diversity index is that it allows the β of a window to be independent of α, and ranging from 1 (if pixels are identical) to the size of the window, 9 (if pixels are fully dissimilar). Therefore the β values of windows with contrasting mean α-diversity values are still comparable (i.e. equivalent numbers, Jost 2007).

Efficiency of the current protected area network

We finally tested the efficiency of the current protected area network to safeguard species and diversity facets under current and future conditions. Analyses were performed at two protection levels: 'truly protected' areas ([Ia, II, III, IV and Natura2000]); and protected areas with sustainable use of natural resources (V) plus the truly protected areas.

With regards to species, we first estimated to which percentage each species of the study area was protected with regards to its conservation status. In other words, for each 2.5 km pixel we extracted the percentage of area protected, and then calculated the percentage of protected area for each species under current and future conditions (Alagador et al. 2011).

With regards to diversity, a gap analysis was conducted with a complementarity perspective (Faith et al. 2003). More specifically, we up-scaled the protected area network to 2.5 km choosing an arbitrary threshold of 50% (i.e. if a 2.5 km pixel contained ≥ 50% protected area, we considered it as protected). Then, we compared α-diversity in- and outside of the protected area network and calculated the β-diversity between the two areas to investigate the complementarity between the two areas. If the current protected area network were successful in protecting the different diversity facets, then in and outside protected areas would have a similar α-diversity and a β-diversity equals to 1, which is the minimum in the Leinster and Cobbold's (2012) framework. This calculation was carried out under both current and future conditions.

Results

Performance of species distribution models

Overall, the performance of SDMs was high with an average TSS and ROC of about 0.48 and 0.98 respectively (Supplementary material Appendix 2, Fig. A2). Interestingly, rare alpine species were extremely well-predicted according to both measures of performance (median TSS of 0.6 and ROC close to 1). There was no other general trend in performance except that alpine species were usually better predicted than those from lower altitudes. We removed 213 species from the following analyses due to TSS and ROC being below 0.3 and 0.8, respectively. Thus, 2542 species were examined below.

Species' sensitivity to climate and land cover change

In general, species' sensitivity to both climate and land cover changes differed between altitudinal vegetation belts and in respect to species' conservation and rarity status, but irrespective of regional climate models, climatic scenarios, or land cover scenarios (Fig. 2 for the A1B – GRASS scenario, Fig. A3, A4 and A5 in the Supplementary material Appendix 2 for the remaining RCMs and scenarios). Colline species were always predicted to experience an increase in suitable habitats due to a strong increase in suitable climate at higher altitudes, while lower altitude bands remain suitable. Species from the other altitudinal vegetation belts were generally

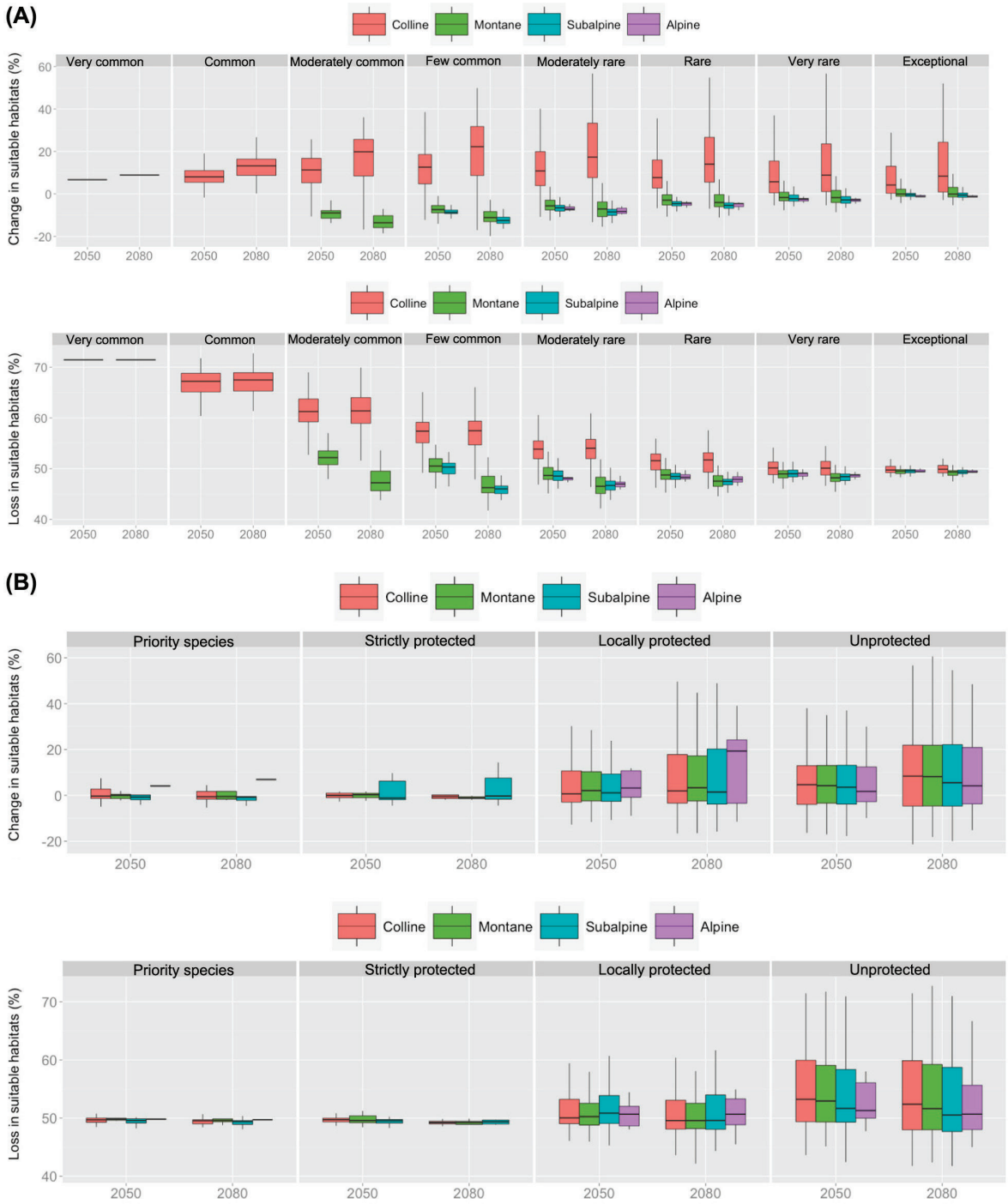

Figure 2. Species sensitivity to climate and land cover change by 2080 with respect to their rarity-commonness value (A) and their conservation status in the study area (B). Results are ordered by altitudinal belts to which the species belong. Up and lower panels differ in the measure of sensitivity. Up panels represent change in suitable habitats (CHS), while lower panel represents loss in suitable habitats (LHS) by 2080 (HadCM3/HadRM3 driven by the A1b scenario and the GRASS storyline).

predicted to have moderate change in suitable conditions (CHS, Fig 2A – top panel) although they were, in general, predicted to loose a fair amount of currently suitable areas (LSH, Fig. 2A – lower panel, 48% on average), which is likely due to the general decrease in area with increasing altitude. If those species are not able to migrate toward more favorable conditions, they will be under strong threat. Interestingly, when going from moderately rare to exceptionally rare species, the predicted loss in environmental suitability decreased (LSH, Fig. 2A – lower panel). In other words, extremely rare species are not predicted to experience a drastic loss in suitable conditions.

This was mirrored when considering the protection status of species (Fig. 2B). Most unprotected species were predicted to expand their suitable area (CHS, Fig. 2B – top panel, e.g. usually common species from the lowlands) whereas species

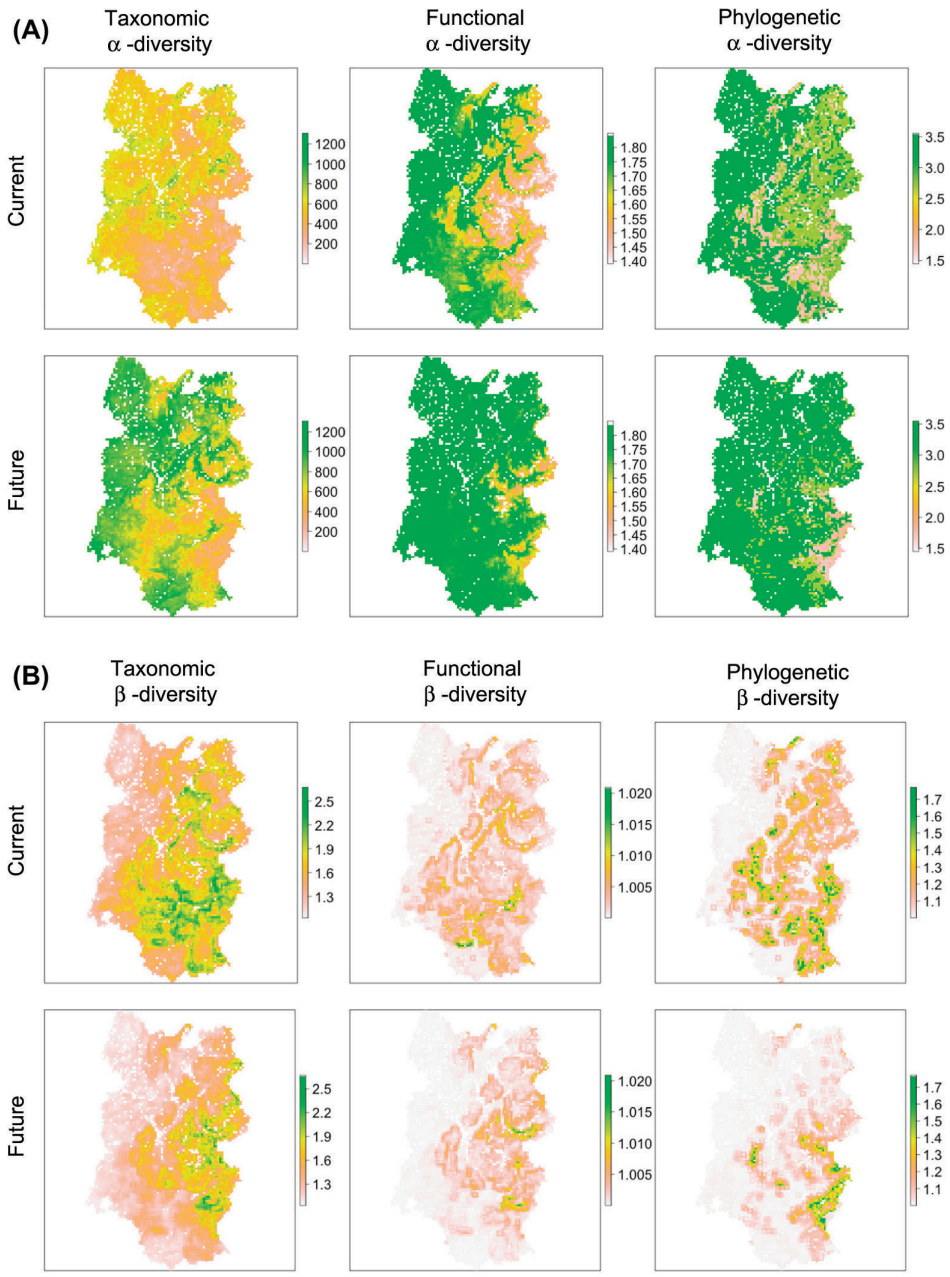

Figure 3. Spatial patterns in α-diversity (A) and β-diversity (B) with parameter *q* equals to zero (presence–absence) for the three facets of plant diversity and under current and future conditions by 2080 (HadCM3 × HadRM3 driven by the A1b scenario and the GRASS storyline).

with strict and top priority protection were not predicted to be strongly affected by the modeled climate and land cover changes (Fig. 2B) top and lower panels).

Mapping of taxonomic, phylogenetic and trait diversity across space and time

Patterns of α- and β-diversity differed spatially and in response to climate and land cover changes by 2080 (Fig. 3 and Supplementary material Appendix 2, Fig. A6, A7 and A8). Under current conditions, there was a less pronounced variation in taxonomic α-diversity across the French Alps than in phylogenetic and functional diversity, whereas this patterns was reversed for β-diversity. Interestingly, even if they are somehow correlated to taxonomic diversity, both phylogenetic and functional α-diversity were relatively high in the low-lands (western French Alps) and only decreased in the high mountain areas where national parks are located (Fig. 1). Functional α-diversity showed a more marked spatial pattern than did phylogenetic α-diversity, which did not vary strongly throughout the French Alps, certainly because most of the main angiosperm clades are occurring throughout the study region. However, phylogenetic β-diversity showed a more marked pattern than did functional β-diversity, with high turnover in ecotones between low land and high mountains zones (Fig. 3B).

Under climate and land cover changes (here using the HadCM3/HadRM3 models driven by the A1b emission scenario and GRASS storyline), the spatial patterns tended to change more drastically for taxonomic than for both functional and phylogenetic α-diversity. Taxonomic α-diversity was predicted to increase almost everywhere while still decreasing from lowlands to high mountains. For the other two facets, we observed a strong increase in α-diversity at high altitudes. On the contrary, β-diversity was projected to severely decrease for the three facets. In other words, there is a general tendency toward diversity homogenization, except in the very high mountain tops and transition zones between montane and alpine belts. Given the general trends in CSH and LSH, this reflects a migration of species from the lowlands to higher elevations, which tended to increase the functional and phylogenetic α-diversity of the mountaintops. Interestingly, for a same scenario A1B-GRASS, projections diverged in functions of the combinations of GCM × RCM used (Fig. 3, Supplementary material Appendix 2, Fig. A6, Fig. A7). For instance, while change in α- and β-diversity were relatively similar between HadCM3/HadRM3 (Fig. 3) and CLM/ECHAM5 (Supplementary material Appendix 2, Fig. A6), the combination RCA3/CCSM3 led to less severe changes, with overall the same patterns as with the other two climate models, but lower in terms of absolute values. This last combination under the A2 emission scenario and BAMBU storyline when modeled with the RCA3/CCSM3 climatic model gave more drastic changes than under the A1b × GRASS scenarios.

Protected area network in the face of environmental change

When focusing on the existing truly protected network (categories I, II, III, IV and Natura2000), the level of protection clearly met the conservation status of the species (Fig. 4). Priority species were best protected on average (42%) under current conditions, followed by species strictly protected (38%). Despite this high average protection, 13 of the 48 priority species and 10 of the 39 strictly protected species have less than 25% of their range protected. Species locally protected or without any conservation status were, on average, not very well covered (23 and 18% respectively) by the network, possibly due to their generally larger ranges. The same trends were predicted under future conditions (Fig. 4). Interestingly, priority species were predicted to even increase the proportion of their protected range under future conditions despite the comparably high variability among RCMs and scenarios. The pattern was somehow consistent for strictly protected species (except under two A1b RCMs scenarios, Fig. 4). Species locally protected or unprotected were not predicted to have any significant change in their level of protection. Patterns were similar when considering all protected areas in the French Alps ([Ia, II, III, IV, V and Natura2000]; Supplementary material Appendix 2, Fig. A9).

When considering the overall protection of the different diversity patterns we observed no turnover between the three facets' diversities in- and outside of the protected areas, under both current and future conditions (results not shown as β-diversity was always equal to 1 when comparing the three diversity facets in and out of the protected area network). In other words, the spatial distribution of the protected area network in the French Alps generally protects the three facets of diversity well and seems well positioned to keep doing so in a near future. The fact that a quite large number of species have less than 25% of their range protected tempers this positive result and highlights that protecting diversity as a whole does not necessarily mean that individual species are well protected.

Discussion

Summary of the main findings

Here we demonstrated the promise of generating biodiversity scenarios for several facets of biodiversity together within the same modelling framework. Such an approach is needed to complying with different conservation options, that put more emphasis on species richness, the functioning of ecosystems, or the evolutionary history of biota, and that are able to contrast these options across geographic space and a protection network. By doing so, future conservation actions can be designed to better fit some of these conservation options and better compensate projected alteration of ecosystem functioning or projected loss of particular phylogenetic lineages.

In this paper, we asked whether projected climate and land cover change would strongly influence the potential suitable habitats of plant species and the spatial patterns of diversity facets in the French Alps, and ultimately whether current reserve network would adequately protect biodiversity given projected changes. The short answer is yes, but not necessarily as expected. Indeed, although the currently suitable climate and land cover is going to shrink for a large portion of species, new suitable areas still seem to be available for many of them. Obviously, these newly suitable habitats, generally available at higher altitudes, would have to be reached and this will heavily depend on the capacity of species to migrate fast enough to keep track with their preferred conditions (Dullinger et al. 2012). Reciprocally, the supposedly 'lost' conditions should not be interpreted as 'immediate local extinction' as it will depend on plant longevity, their tolerance to climate variability (Zimmermann et al. 2009, Dullinger et al. 2012) and competition from immigrating species (Svenning et al. 2014).

Nevertheless, species from different altitudinal-vegetation belts show opposing patterns. Species from the montane vegetation belt are projected to have a decrease in suitable area. This result certainly has to do with mountains topography as migrating up-ward necessarily means reducing range areas. However, why do species from subalpine and alpine belts not show the same pattern? Indeed, those species, generally rare, are projected to be much less affected by climate and land cover changes than others. We hypothesize here that calibrating the species models at very high spatial resolution allowed us to capture the fine-scale relationships between plant species from high altitude and their meso-scale environment (Randin et al. 2009) and that high alpine species may potentially tolerate wider climatic fluctuations than previously thought (but see Beaumont et al. 2011).

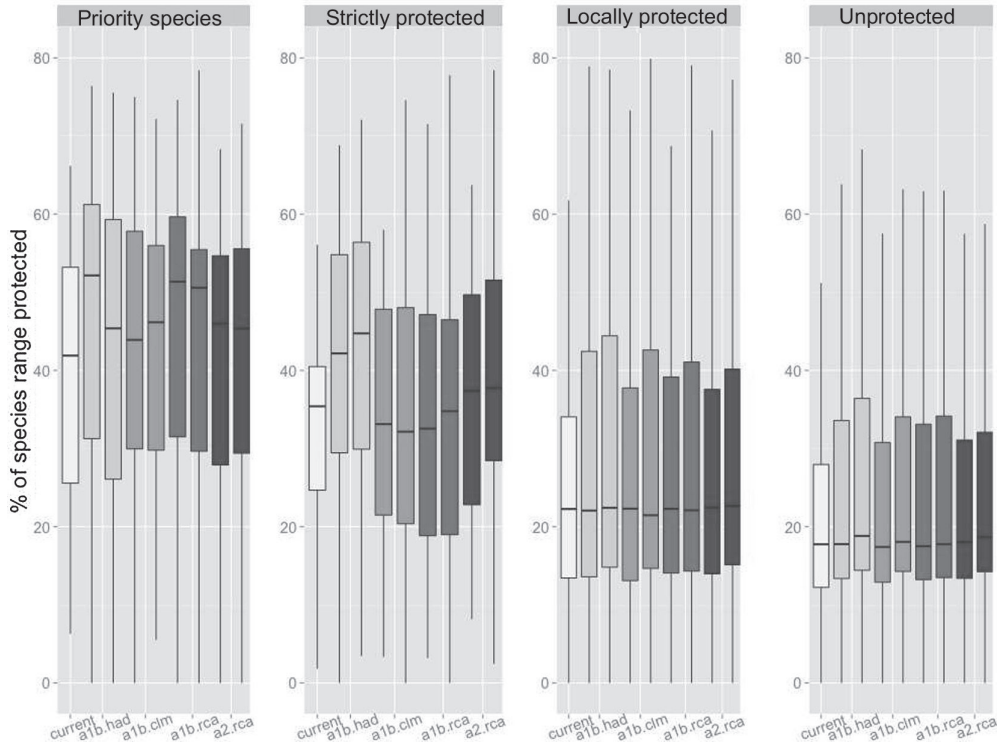

Figure 4. Level of species protection over the French Alps under current and future conditions by 2050 and 2080 with respect to species conservation status. Y-axis represents the percentage of species ranges that are protected, over all species from a given conservation status (i.e. priority species, strictly protected, locally protected, unprotected). The x-axis represents the current and future conditions. For each future condition (i.e. a given color for a given name), there are two bars, one for 2050 and one for 2080 (from left to right). Abbr.: A1b.had: HadCM3/HadRM3 climate model driven by the A1b scenario and the GRASS storyline. A1b.clm: ECHAM5/CLM driven by the A1b scenario and GRASS storyline. A1b.rca and A2.rca: CCSM3/RCA3 climate model driven by the A1b and A2 scenarios and the GRASS and BAMBU storylines, respectively. The protected area network corresponds here to truly protected' areas (Ia, II, III, IV and Natura2000).

The protected area network seems very efficient to protect extant plant diversity under current conditions in the French Alps. Our modeling analyses also suggest that it will continue to do so in the future, and likely even protects more species and more diversity under changed environmental conditions. This result is in contradiction to previous studies at large spatial scales from mostly lower altitudes, where large areas are covered by similar vegetation. For instance, Araújo et al. (2011) suggested that around 58% of European plant and terrestrial vertebrate species could lose suitable climate in protected areas, whereas losses affected 63% of the species of European concern occurring in Natura 2000 areas. Our analysis on the French Alps does not corroborate those general European findings, suggesting: a) that multi-scale assessments are of interest to contrast regional vs continental situations, and b) that higher altitudes with a rich habitat diversity might be less affected by environmental change than are lowlands. In the French Alps, most of the protected areas are located in remote, high altitude areas and span a large elevation gradient. The three main National Parks have 81% of their area above 2000 m a.s.l. These high altitude areas are also the ones projected to provide suitable climate and land cover to more species in the future, with an upward migration of species from lowlands. Obviously, the extinction debts of species due to long-term dynamics, biotic interactions and limited dispersal might modify this pattern (Van der Putten et al. 2010, Dullinger et al. 2012) but it is reasonable to assume that high altitudinal protected areas will gain species and diversity under these changing conditions. Glacial retreats are already providing more space for high altitude species (Burga et al. 2010), and will thus probably buffer the negative impacts of competition from immigrating species from lowlands (Carlson et al. 2013).

Our multi-facets framework allowed us to forecast that the spatial distribution of taxonomic, functional and phylogenetic diversity in the French Alps will probably change drastically. Indeed, although the α-diversity should in general increase in most of the area (invading plant species from lowlands) and should also be well protected, the β-diversity is expected to strongly decrease for all three diversity measures. Interestingly, the general patterns generally fit our expectations. Changes in species diversity in response to future scenarios were much more pronounced than for the other two diversity facets. As also expected, the current spatial pattern of phylogenetic diversity was already quite homogenous under current conditions, and this homogenization was predicted to increase in the future. Similarly, functional diversity at moderate to high altitude was also predicted to increase in the future due to the arrival of migrants from lower altitudes with new sets of traits. On the one hand, this is a rather positive output as, for instance, an increase of functional diversity ultimately leads to an increase of ecosystem productivity and resilience (Loreau 2000, Cadotte et al. 2011). This is especially true in our case where we selected

four traits known to have strong relationships with ecosystem functioning. For instance, Garnier et al. (2004) showed that specific leaf area was a strong marker of primary productivity and litter decomposition rate. More generally, it also means that, with climate and land cover change, we can expect to see a higher diversity of plants in terms of the leaf-height-seed plant ecological strategy scheme, thus encompassing a wide range of functions. The same conclusion holds for plant phylogenetic α-diversity that has been shown to be a robust predictor of productivity and stability (Cadotte et al. 2012). On the other hand, at regional scale, the projected decrease in β-diversity implies a general trend towards homogenization in diversity across the landscape, with few exceptions at highest elevations.

Uncertainties and perspectives

Although we have tried to incorporate modeling uncertainty through ensemble forecasting of species distributions and through the use of a range of RCMs and emission scenarios, our projections are still subject to various sources of possible errors and should not be interpreted as true forecasts, but rather as a projection of general trends instead. We have used correlative species distribution models that account for dispersal and biotic interactions in a very indirect way (Guisan and Thuiller 2005). The non-explicit inclusion of these important processes on range dynamics causes uncertainties when modeling species ranges at high spatial resolution under environmental changes (Van der Putten et al. 2010, Thuiller et al. 2013). Recent metacommunity models suggest that local species extinction in changing environments are strongly enhanced by negative biotic interactions (Norberg et al. 2012), and that overlooking biotic interactions would cause models to over-predict future species prevalence. Nevertheless, biotic interactions have been shown to mostly influence the spatial variation in species' abundance rather than occurrence in the French Alps (Boulangeat et al. 2012). Because of these potential sources of errors, we did not interpret our results at the resolution at which we gathered and calibrated the models. Instead, we optimized the spatial resolution at which the pervasive effects of dispersal, history and biotic interactions were less influential on projected biodiversity distribution patterns (Supplementary material Appendix 2, Fig. A1). This is especially true for topographically very heterogeneous regions such as the French Alps, and may not be sufficient to overcome these problems for large flat lowland areas. By comparing observed and modeled species richness from simple stacking of individual species projections, we found that correlative SDMs did also well in projecting species richness when degrading the resolution to 2.5 or 5 km. We are thus relatively confident that the detected patterns are robust with respect to the underlying hypotheses of correlative SDMs. However, the development of distribution models for alpine plant species incorporating a number of fine scale ecological processes is definitely an important task (Carlson et al. 2013).

An additional issue of our analysis concerns the relatively static view of biodiversity. Indeed, we considered effects of environmental change on plant diversity in the French Alps. In an era of environmental change, species from the Mediterranean area will obviously migrate and invade the southern French Alps, while more temperate species from the west of France will most likely immigrate into the Alps. This does not influence the analyses of species ranges but it could certainly influence the resulting patterns of biodiversity facets. For instance, changes in taxonomic α-diversity at the edge of our study area are certainly misleading and an influx of species not yet present in the French Alps would certainly increase species richness and decrease the predicted homogenization (Fig. 3). Obviously, the migration of exotic species from abroad or species from very different clades would have an influence of the overall patterns but the effect will be rather minor given that a high number of major plant clades are already present; for instance, in the French alpine flora there are representatives of 150 plant families (compared to 415 families in the world according to APG III). Indeed, when considered at regional scale, naturalized exotic species tend to belong to the same families or lineages as the ones already occurring in the recipient region (Thuiller et al. 2010).

Conclusion

Climate and land cover changes are projected to modify the spatial distribution of plant species and plant diversity in the French Alps. Although the most common species are projected to experience drastic changes in their suitable habitats, rare species seem to be much less affected by projected environmental changes, mostly because they occupy specific meso-scale environmental conditions at very high altitude that remain to be present in the future. Most importantly, those species should be equally well protected under environmental change as they are now. Our gap analysis demonstrates that threatened species or species of conservation interest are well-protected under current conditions, and remain to be so in the future. Our models indicate that the spatial patterns of plant diversity of the three facets (taxonomic, phylogenetic and functional) will be severely modified. Overall, although the patterns of change are not necessarily overlapping across the three types of diversity, local α-diversity is generally predicted to increase at the cost of β-diversity. Most of the changes are projected to occur at the mid-altitudinal vegetation belts, which represent the ecotone between lowland and high altitude vegetation strategies. To the best of our knowledge, this is the first complete risk assessment carried out over a comprehensive region, combining up-to-date climate, land cover and species distribution models, together with a multi-facet view of plant diversity. More regional risk assessments are needed to effectively test the efficiency of current protected area networks in this era of drastic changes.

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Supplementary material (Appendix ECOG-00670 at <www.oikosoffice.lu.se/appendix>). Appendix 1–2.

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